THE UNIVERSITY OF ALBERTA

GENERAL ACTIVITY AND MAINTENANCE BEHAVIOR OF COYOTES IN CAPTIVITY

by

© LEONARD WALDEMAR MOTTUS

A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "General Activity and Maintenance Behavior of Coyotes in Captivity", submitted by Leonard Waldemar Mottus in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

General activity and maintenance behavior of six captive coyotes (Canis latrans) was studied near Edmonton, Alberta.

The general activity was associated with several meteorological elements. The animals were diurnal in their activity pattern, with the peak of activity occurring shortly after dawn. The highest levels of activity occurred at 30 to 60^{o}F, low relative humidity, and low barometric pressure, with pressure influencing activity the most. Winds of less than 14 miles per hour stimulated activity, while winds of more than 14 miles per hour reduced activity, especially if accompanied by a falling pressure. The possibility of a lunar influence on barometric pressure and general activity was also discussed.

Maintenance as a non-social behavior exhibited by coyotes in captivity was studied primarily in one litter (two males and one female).

Meteorological elements appeared to be of secondary importance in the location of the bed site, with the structural characteristics of the cage being most important. The behavior associated with lying down was discussed.

The significance of scratching, biting, and licking was presented. No self-grooming patterns of rubbing or rolling were observed.

Elimination in captivity appeared to occur at a reduced frequency, probably because of the lack of novelty in the

cage. Pre-elimination exploration suggests that both sexes are involved in scent marking. The postures of elimination are similar to those of the domestic dog (<u>Canis familiaris</u>), although the males never displayed the leg-lifting posture of urination. Urination sites appeared to be randomly distributed, while defecation sites appeared to be located away from the bed site.

ACKNOWLEDGEMENTS

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INTRODUCTION

The first recorded reference to the coyote was in 1780, when Clavijero (cited by Dobie, 1961, p. 32) wrote that it "is one of the most common quadrupeds of Mexico, in form like the dog, voracious like the lobo, astute like the fox, in some qualities resembling the jackal." Subsequently, several authors have presented detailed descriptions on certain phases of the coyote's life history. The economic status of the coyote has been studied by Murie (1940), Young and Jackson (1951), and Gier (1957). Sperry (1941) made a study of the food habits of the coyote, while the morphology of this animal has been described by Young and Jackson (1951). Methods of controlling the number of coyotes have also received a great deal of attention (Young and Jackson, 1951; Gier, 1957). Information on the habits and behavioral characteristics of the coyote (Murie, 1940; Young and Jackson, 1951; Van Wormer, 1964), however, are limited in detail, being based on few observations, or on second-hand information. This lack of information on the behavior of coyotes is probably associated with the difficulty of obtaining prolonged observations of known animals. For this reason, I utilized captive coyotes and concentrated the study on general activity and maintenance behavior.

The first part of this thesis was to search for associations between general activity of coyotes in captivity and various meteorological elements. Past research on activity patterns of mammals appear to be concentrated primarily on

circadian rhythms in activity (Bider, 1962) and on the association between barometric pressure and activity (Brown, Webb, and Macey, 1957; Sprott, 1967). This study will search for possible correlations between general activity of coyotes in captivity and several meteorological elements (photoperiod, temperature, relative humidity, barometric pressure, wind, season, and the moon). An attempt will be made to determine which of these elements exhibit the best association with general activity of the study animals.

Maintenance as a non-social behavior in canids has been studied by several authors. Scott and Fuller (1965) have made an extensive study on the domestic dog, while the wolf (*Canis lupus*) has received the attention of authors such as Murie (1944), Rutter and Pimlott (1968), and Young and Goldman (1944). Tembrock (1957, cited by Scott and Fuller, 1965) has studied the fox (*Vulpes vulpes*), but for some reason little work has been done on the coyote. Murie (1940) has reported a few elements of the maintenance behavior of coyotes, and Snow (1967) has studied coyote pups in captivity, but detailed information on the individual behavior of adult coyotes was unavailable. The second object of this thesis was to fill this gap in the knowledge of canid behavior by presenting information on the maintenance behavior exhibited by coyotes in captivity. Behavior associated with ingestion was omitted because it was consistent with the behavior patterns that Scott and Fuller (1965) described for the domestic dog.

METHODS

The Animals Studied

This study, initiated in July, 1967 and completed one year later, involved the use of 6 coyotes held in captivity. These animals were obtained from 3 different litters born in the vicinity of Edmonton, Alberta. The coyotes which were obtained from each litter were:

1. Two juvenile males and one female (D, F and E, respectively) were obtained from a local farmer on July 3, 1967.
2. Two juvenile females (B and C) were obtained from the Zoology Department of the University of Alberta, Edmonton, on July 10, 1967. These pups were donated to the University by a local farmer.
3. One yearling female (A), which had been a family pet, was obtained on July 12, 1967.

Identification of the Animals

Individual animals were identified through morphological peculiarities. Since the different litters were housed in separate cages, this problem was minimized.

Coyotes B and C were easily separated because coyote B had a left wrist which was enlarged. This enlarged joint appeared to be the result of an early fracture.

Coyotes D, E and F were easily separated because coyote E had a slot in the medial edge of its right ear (when directed

forward), and coyote F had a slot at the tip of its right ear.

Housing the Animals

The coyotes were housed and studied in an outdoor enclosure located at the Bio-Science Vivarium, 6 miles south of Edmonton, Alberta. The enclosure, measuring 20 by 30 feet, was subdivided into 3 equal cages measuring 10 by 20 feet. These cages were visually isolated from each other by a 4-foot-high plywood wall (Fig. 1).

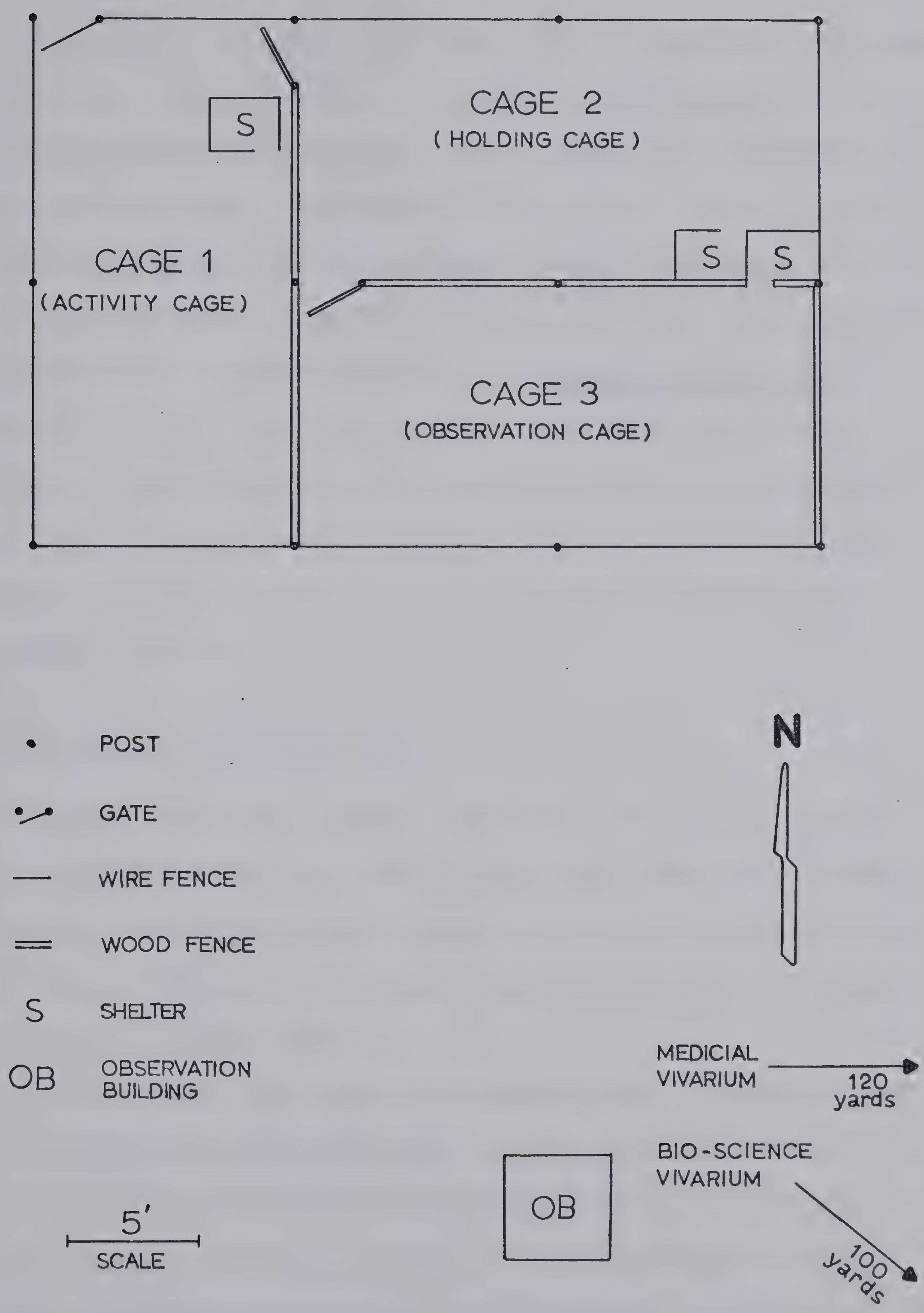
The cage was built with a wooden frame and stucco-wire covering. Wire covered the sides, ground, and a 2 foot overhang on the top of the walls. The floor was covered with straw during winter, and with sand and gravel during summer. Shelter was provided.

Diet and Disease

The coyotes were fed a mixture of a high quality dog meal and ground horse meat. Equal quantities of each were mixed, soaked with water, and frozen in six cup packages. These packages contained approximately two pounds of the mixture which two animals could nearly consume in one day. The animals were fed daily, at my own convenience, while in their individual cages.

Bones were provided for gnawing, and any unwanted chickens or mice from the vivarium were also fed to the coyotes. During summer, grass was regularly placed in the cage, because the animals were often seen eating grass at the

Fig. 1. Floor plan of the outdoor enclosure located at the Bio-Science Vivarium.



CAGE 2
(HOLDING CAGE)
S
S
S
CAGE 1
(ACTIVITY CAGE)
CAGE 3
(OBSERVATION CAGE)
POST
GATE
WIRE FENCE
WOOD FENCE
S SHELTER
OB OBSERVATION BUILDING
5′
SCALE
N
MEDICIAL VIVARIUM
120 yards
BIO-SCIENCE VIVARIUM
100 yards
OB

edge of the cage. Water was provided in summer and snow in winter.

The risk of disease and parasites was minimized by keeping the cages free of feces. Biannual examinations of the feces by the method of Levine et al. (1960) for internal parasites were negative. All animals were given injections for distemper and hepatitis three weeks before the study started.

The only parasite problem encountered was the presence of what appeared to be mange mites (*Sarcoptes scabiei*). Coyotes D, E and F had a heavy infection when they were obtained. The condition soon appeared in coyote A, but was never exhibited by coyotes B and C. Attempts to eliminate this ecto-parasite with chemicals failed. The infection eventually subsided.

Sources of Meteorological Data

Temperature and relative humidity data were obtained from a hygrothermograph at the study site. This instrument was located in a Stevenson's screen on the ground beside the cage. This placed the recording elements of the instrument at the level of the coyotes.

Data on wind and hours of sunshine were obtained from a field station of the University of Alberta located approximately one-half mile south of the Bio-Science Vivarium.

Barometric pressure readings were obtained from the Edmonton International Airport, approximately eight miles south of the cage.

Records of solar and lunar cycles were obtained from the Coronation Park Planetarium in Edmonton.

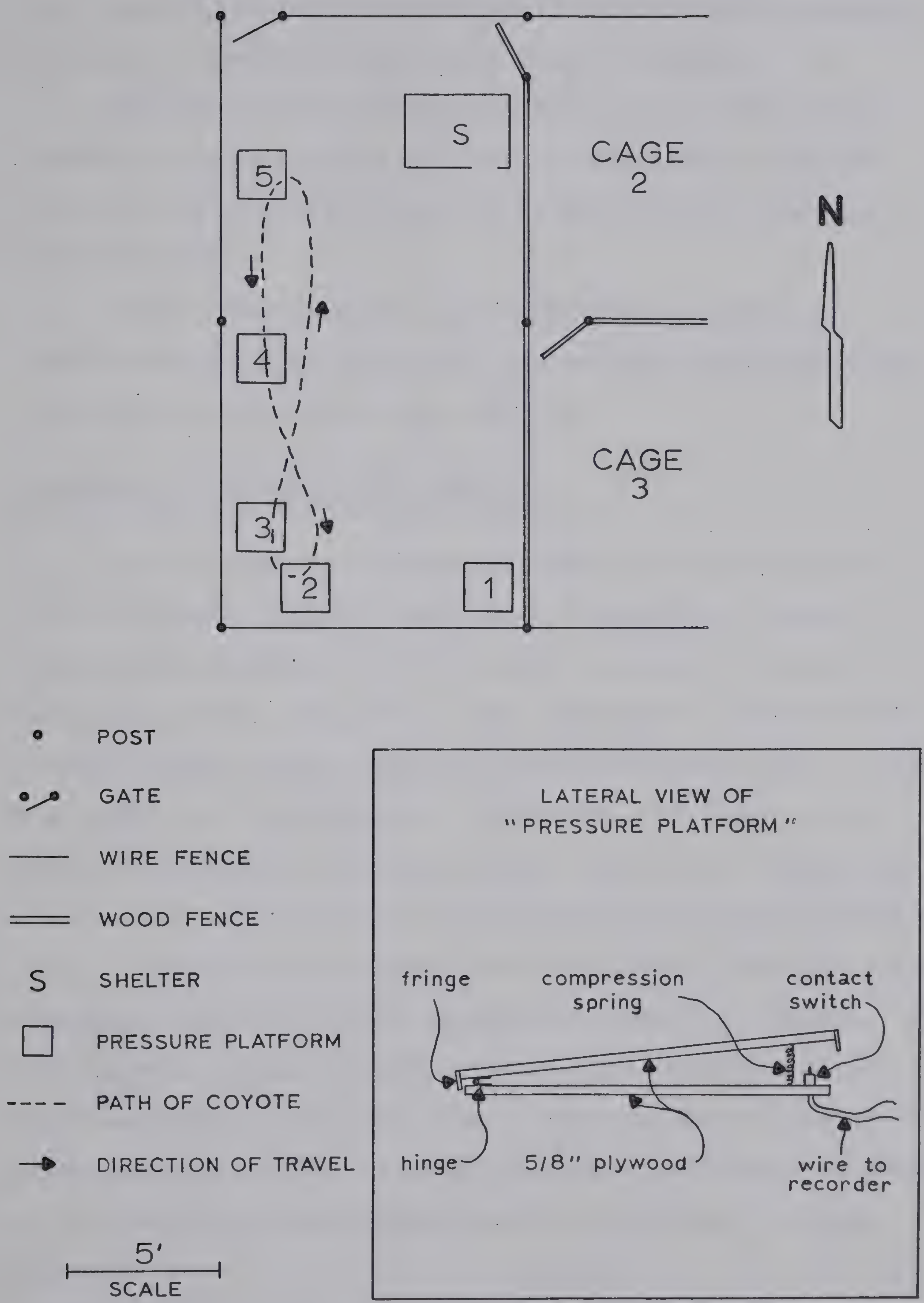
Technique of Recording Activity

Only one coyote was used to record general activity. Coyote A developed a sterotyped behavior (Hediger, 1964) of pacing beside the west fence of cage 1 (Fig. 1). Recording the occurrence of this pattern involved the placement of "pressure platforms" along the route travelled (Fig. 2). These platforms were constructed of two pieces of 5/8 inch plywood. The upper board was 18 inches square and the lower board was 17 inches square. The boards were centered and hinged. A contact switch was installed near the free-edge, and a compression spring was placed near it. A 1-1/4 inch fringe on the upper board prevented the entry of foreign objects between the boards. Protruding nails on the lower board anchored the platform to the substrate.

The platforms were connected electrically via 12-volt battery to an Esterline Angus event recorder (Model A620X) located in the heated observation building (Fig. 1). The event recorder had a chart speed of 12 inches per hour, and required servicing every 4 days.

When a platform was stepped on, the contact switch closed the circuit, and the event was recorded. The platform which exhibited the maximum number of events during a 15 minute period was used as the measure of activity. This reduced the possibility of compounding the actual activity,

Fig. 2. Floor plan of cage 1 showing the location of the "pressure platforms" in relation to the path of coyote A, and a lateral view of a pressure platform.


S
CAGE 2
CAGE 3
N
5
4
3
2
1
POST
GATE
WIRE FENCE
WOOD FENCE
S SHELTER
PRESSURE PLATFORM
PATH OF COYOTE
DIRECTION OF TRAVEL
5′
SCALE
LATERAL VIEW OF "PRESSURE PLATFORM"
fringe
compression spring
contact switch
hinge
5/8" plywood
wire to recorder

since one or several platforms could be stepped on during a circuit. The hourly totals were then calculated.

The presence of visitors at the cage brought about extremes in the activity of coyote A. To reduce this bias, the activity recorded during all known visits to the cage was discarded.

Daily tests were made of the recording apparatus. If any of the platforms failed to record, the data in the period from the preceding test were omitted.

Evaluation of the Recording Method

In an attempt to demonstrate that the recorded data were a reliable index of the general activity of coyote A, the periods of general activity and inactivity of coyote A were observed for 100 hours. These 100 hours occurred during 27 observation periods randomly distributed from 0400 to 2100 hours over the period May 12, 1968 to June 2, 1968. The observation periods ranged in length from 2 to 5 hours with the occurrence of activity setting the final hour of observation, if this occurred beyond the first hour. Activity during the first hour limited the observation period to 2 hours. The last 2 hours of observation were utilized in this analysis. The observations were made from a temporary blind located 100 yards south of cage 1. This distance was sufficient to permit me to enter the blind without causing the animal to become active.

* 9A follows

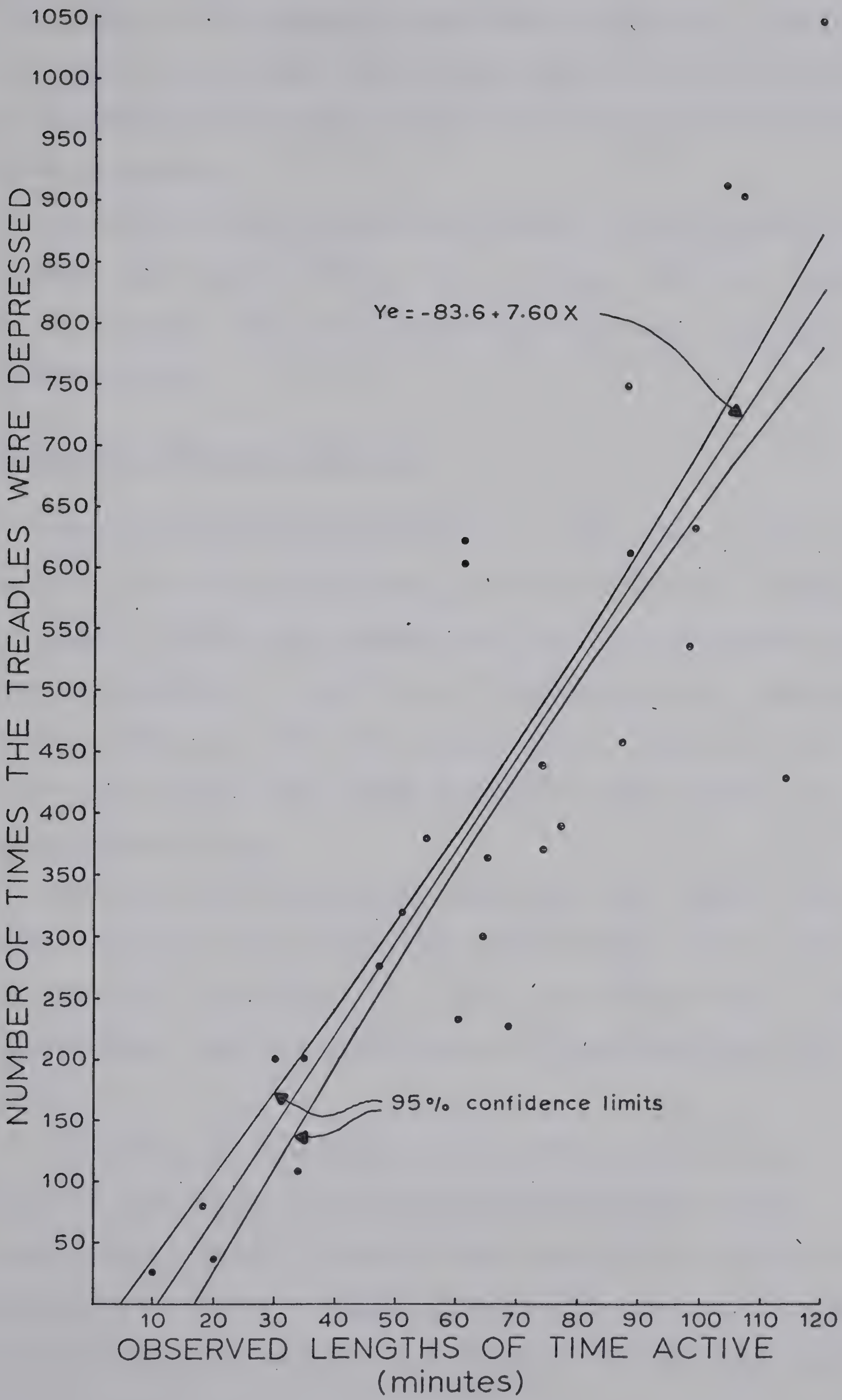
When the observed periods of general activity were compared with the recorded activity (Fig. 3), a correlation coefficient of +0.8492 was obtained. This is highly significant and indicates that the recorded data were a reliable index of the general activity of coyote A at the time of the test.

The possibility that coyote A did not consistently display the stereotyped pattern utilized in recording the data was examined during the study period. Casual observations from the Bio-Science Vivarium (Fig. 1), and examinations of the tracks left in snow after a nights activity suggested a high degree of consistency in the pattern. The repetitious and geometrical character of the path of coyote A was similar to the stereotyped patterns described by Hediger (1964).

The coordination of activity patterns between different animals housed at the enclosure was not analysed at the time of the study. In an attempt to demonstrate that the periods of general activity of coyote A were similar to the periods of activity of the coyote population housed at the enclosure, the periods of activity and inactivity of coyote A were compared with those of coyotes D and E. During the period May 10, 1969 to May 19, 1969, the animals were housed in separate cages and observed for 50 hours from the Bio-Science Vivarium (Fig. 1). The resultant data (Appendix 1) exhibit no statistically significant difference between the total time of observation and the time that coyotes A, D and E were active or inactive together. This suggests that the general activity

Fig. 3. Recorded versus observed activity of coyote A during 27 observation periods randomly distributed between 0400 and 2100 hours over the period May 12, 1968 to June 2, 1968.

* 9A precedes



NUMBER OF TIMES THE TREADLES WERE DEPRESSED
1050
1000
950
900
850
800
750
700
650
600
550
500
450
400
350
300
250
200
150
100
50
Ye = -83.6 + 7.60 X
95% confidence limits
10
20
30
40
50
60
70
80
90
100
110
120
OBSERVED LENGTHS OF TIME ACTIVE
(minutes)

of the three study animals at the time of the test. Casual observations during the study period supports the possibility that the different animals at the enclosure exhibited similar periods of activity.

The statistical procedures involved in this section are from Steel and Torrie (1960). In all cases, the null hypothesis was rejected when the probability level was less than or equal to 0.01.

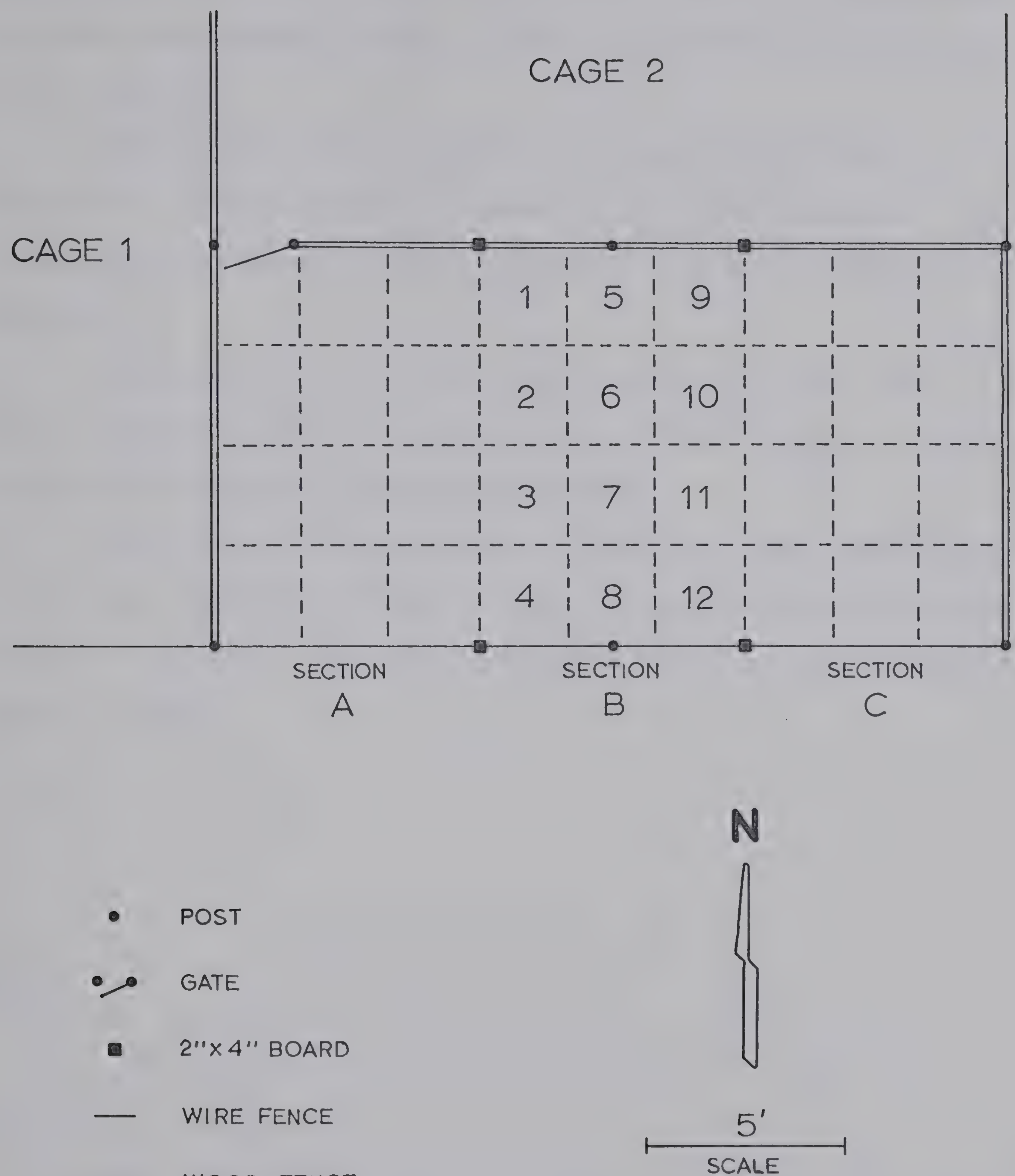
Technique of Studying Behavior

The behavioral observations were made from an observation house located approximately 25 feet from cage 3 (Fig. 1). Cage 3 had a 4-foot-high plywood wall on 3 sides to minimize visual distractions. Cage 2 was a holding cage for animals not being observed. The shelters in cages 2 and 3 had an entrance into both cages which simplified the transfer of animals between cages.

Recording the spatial position where the various behavioral patterns were manifested involved the utilization of an imaginary grid (Fig. 4). This grid divided cage 3 into 36 quadrangles, each of which measured approximately 27 by 30 inches.

Recording the behavior of the coyotes was done by writing on the moving chart of an Esterline Angus event recorder (Model A620X). With a chart speed of 3 inches per minute and writing in a highly abbreviated fashion, a record was established for as many as 3 animals. An accurate record

Fig. 4. Imaginary grid and numeration utilized in cage 3 to record spatial orientation of study animals.


CAGE 2
CAGE 1
1
5
9
2
6
10
3
7
11
4
8
12
SECTION A
SECTION B
SECTION C
N
POST
GATE
2"x 4" BOARD
WIRE FENCE
WOOD FENCE
5'
SCALE

of the duration of the behavioral patterns was obtained by marking the start of a specific behavior on the paper and then drawing a line on the moving chart until the behavioral pattern was changed. Thus, a line of 15 inches would represent 5 minutes.

Most observations pertained to coyotes D, E and F. Occasional observations were made on the other animals. The observation schedule of this behavioral study is shown in Appendix 2.

Numerous 35 mm. photographs, as well as 1,000 feet of 16 mm. motion picture film were taken to aid in the description of the various patterns exhibited.

The statistical procedures involved in this section are from Steel and Torrie (1960). In all cases, the null hypothesis was rejected when the probability level was less than or equal to 0.05.

RESULTS AND DISCUSSION

General Activity of Coyotes in Captivity

Activity and Photoperiod

Most animals have activity rhythms associated with the daily light-dark cycle (Marler and Hamilton, 1967). These circadian rhythms are exhibited by coyotes in "nature", where high levels of activity are mainly crepuscular, nocturnal, and auroral (Ozoga and Harger, 1966; Van Wormer, 1964; Bider, 1962). This pattern of activity may be associated with the avoidance of man, but Bider (1962) and Ables (1969) suggest that dusk to dawn activity synchronizes the activity pattern of the predator with that of their prey. This suggests that coyotes regulate their periods of activity to the optimum time for obtaining food, and when there is carrion available, the need for synchronized activity patterns should disappear. Since carrion is one of the primary foods of the coyote (Sperry, 1941), it is possible that the circadian rhythm of the coyote may be occasionally shifted away from the dusk-dawn activity pattern. Captivity may reflect this shift, since the need of hunting and capturing food is alleviated, a condition similar to a plentiful supply of carrion in "nature".

To examine the effect of captivity on the daily activity pattern of coyotes the recorded data were grouped according to the hours of daylight with the sunrise-sunset time rounded off to the nearest hour. The resultant data (Appendix 3)

for diurnal, nocturnal, and daily activity exhibit no statistical relationship with the length of the photoperiod. Diurnal activity represented 74 percent of the total daily activity over the year. This shift away from the dusk-dawn pattern presented by Bider (1962) could be associated with the availability of food.

The temporal distribution of activity during the various photoperiods was examined for 7-9, 11-13, and 15-17 hour days. The circadian rhythm exhibited by coyotes during the 7-9 hour photoperiods (Fig. 5) show a high level of activity throughout the daylight hours, with little activity occurring during the night. The activity pattern during the 15-17 hour photoperiods (Fig. 7) exhibited a short peak of activity at dawn, followed by a gradual decline until early afternoon, and a lesser peak just before sunset. Hourly activity during the 7-9 hour night (Fig. 7) was slightly greater than that of the 15-17 hour night (Fig. 5). The activity pattern of the 11-13 hour day (Fig. 6) appears to represent a mid-point between the two extremes.

Activity and Temperature

Orr (1959) found that white-footed mice (*Peromyscus maniculatus*) exhibited the greatest activity in captivity between 40 and 50°F. He also noted that activity decreased at higher and lower temperatures. If this association between ambient temperature and general activity of captive mice is applicable to mice in "nature", it would be advantageous for

Fig. 5. Hourly activity of coyote A recorded during the 7-9 hour photoperiods which occurred over the period July 22, 1967 to June 2, 1968.

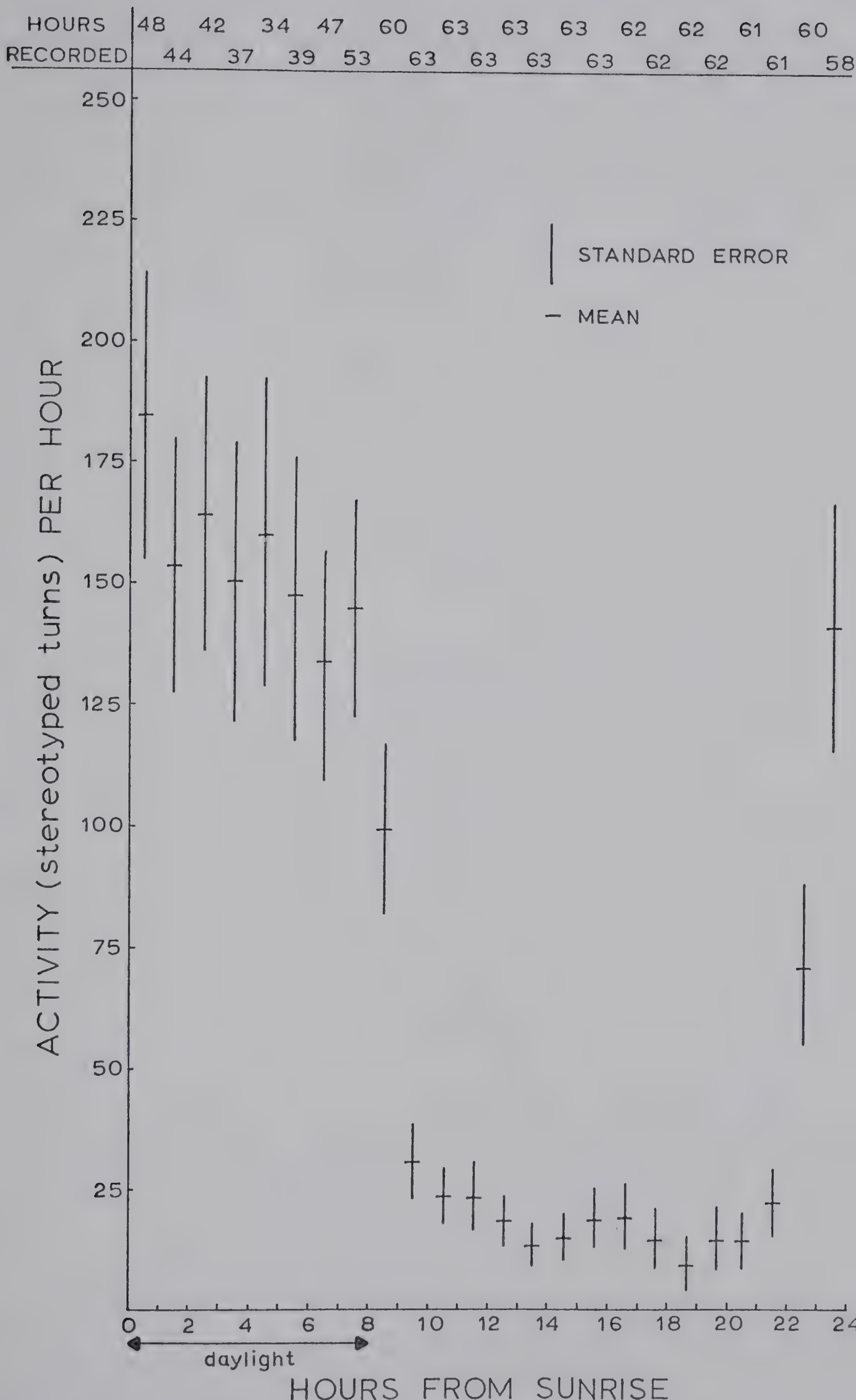
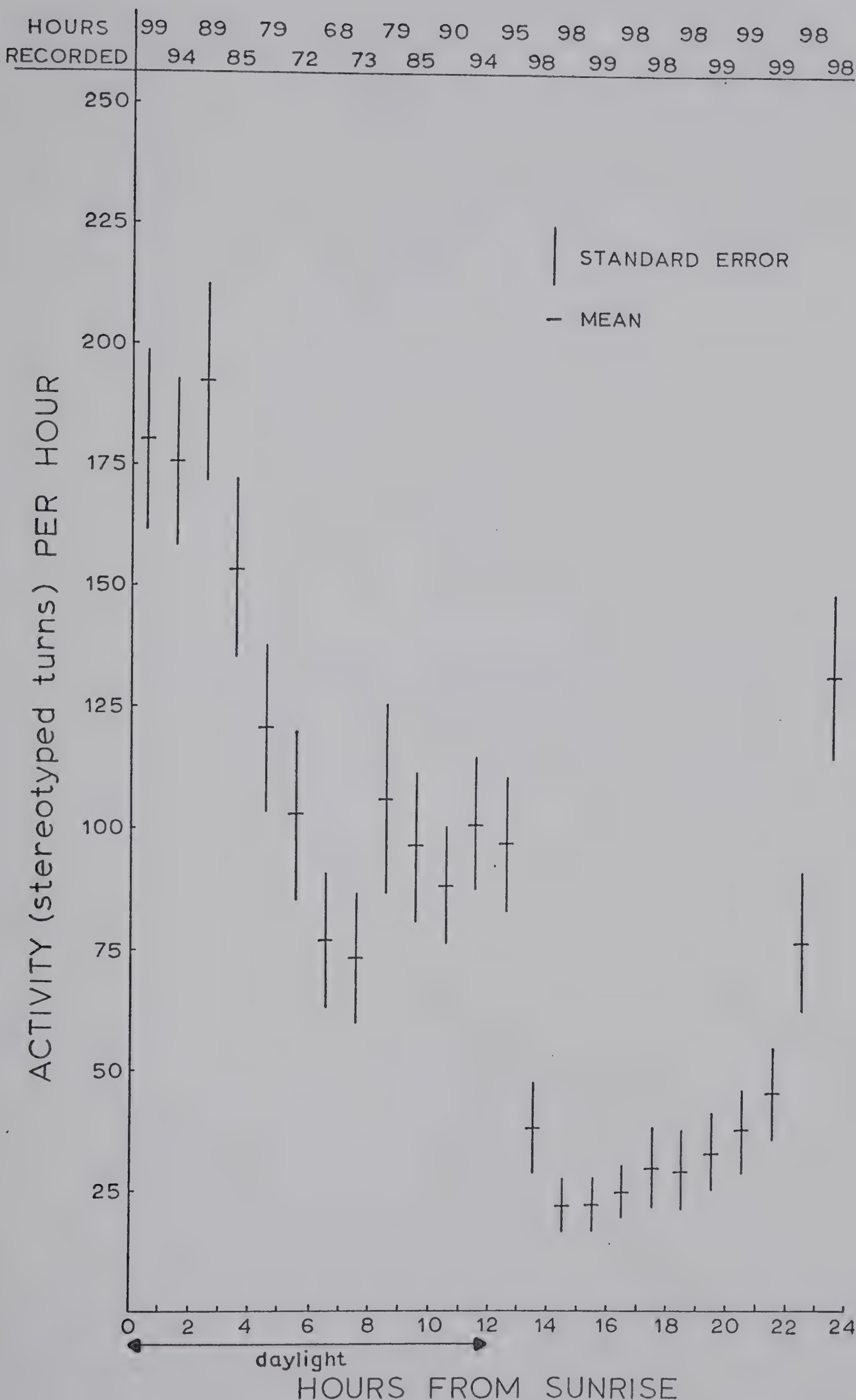
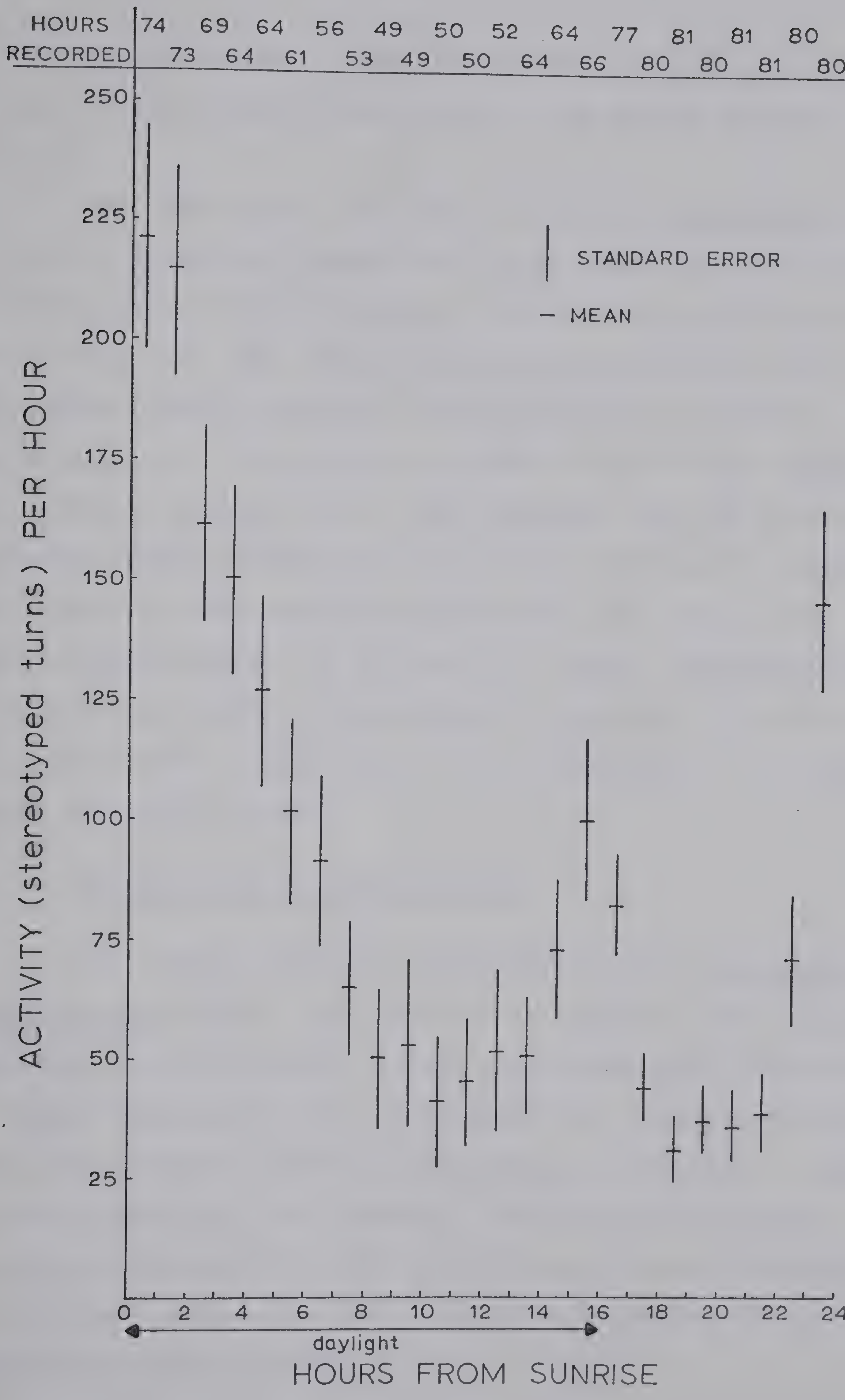

HOURS RECORDED
48 44 42 37 34 39 47 53 60 63 63 63 63 63 63 63 62 62 62 62 61 61 60 58
STANDARD ERROR
MEAN
ACTIVITY (stereotyped turns) PER HOUR
250
225
200
175
150
125
100
75
50
25
0 2 4 6 8 10 12 14 16 18 20 22 24
daylight
HOURS FROM SUNRISE

Fig. 6. Hourly activity of coyote A recorded during the 11-13 hour photoperiods which occurred over the period July 22, 1967 to June 2, 1968.



HOURS RECORDED
99 94 89 85 79 72 68 73 79 85 90 94 95 98 98 99 98 98 98 99 99 99 98 98
250
225
200
175
150
125
100
75
50
25
STANDARD ERROR
MEAN
ACTIVITY (stereotyped turns) PER HOUR
0 2 4 6 8 10 12 14 16 18 20 22 24
daylight
HOURS FROM SUNRISE

Fig. 7. Hourly activity of coyote A recorded during the 15-17 hour photoperiods which occurred over the period July 22, 1967 to June 2, 1968.


HOURS RECORDED
74 73 69 64 64 61 56 53 49 49 50 50 52 64 64 66 77 80 81 80 81 81 80 80
ACTIVITY (stereotyped turns) PER HOUR
250
225
200
175
150
125
100
75
50
25
STANDARD ERROR
MEAN
0 2 4 6 8 10 12 14 16 18 20 22 24
daylight
HOURS FROM SUNRISE

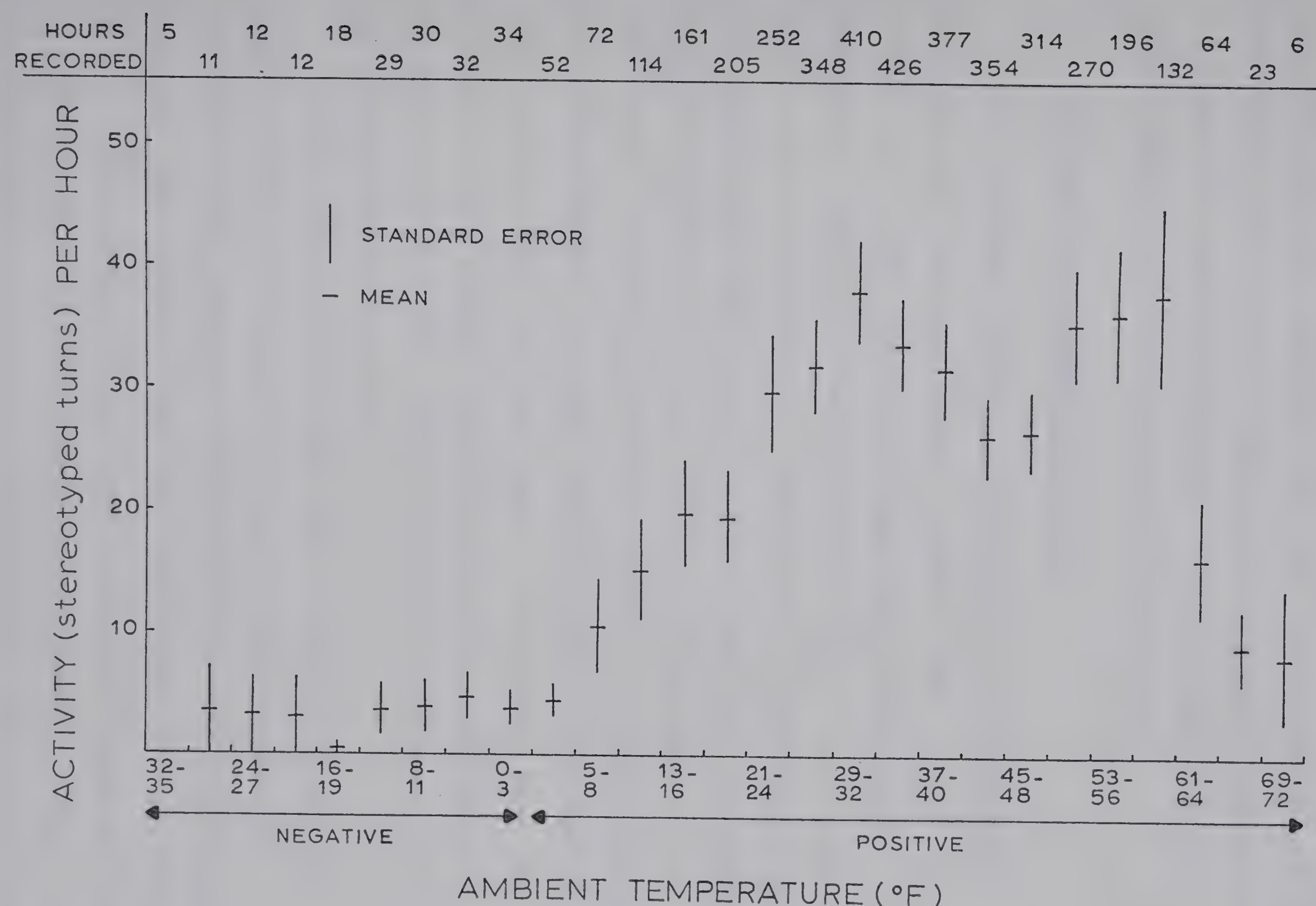
the coyote to exhibit a similar pattern of activity, since mice are one of the primary foods of the coyote (Sperry, 1941).

When the general activity of coyote A was examined in relation to ambient temperature, there was a trend toward a bimodal curve with the peaks of activity occurring at 30 and 60°F (Fig. 8). The slight reduction in activity at 45°F is not significantly different from the peaks of activity, although it is significantly different from the low levels of activity at 0 and 70°F. This suggests that the association between ambient temperature and general activity is similar for both mice and coyotes in captivity, with coyotes exhibiting high levels of activity in a wider temperature range. If this relationship is maintained in "nature", it would be to the coyote's benefit, since the predator would be active when the prey is active.

Activity and Relative Humidity

Orr (1959) states that white-footed mice (*Peromyscus maniculatus*) exhibit more activity in captivity when relative humidity is high, but not at the saturation point, than when relative humidity is low. The possibility coyotes exhibit the same activity pattern in captivity, in relation to the relative humidity, was examined. Data used were obtained between 2200 and 0300 hours to avoid any influence from the sun. The influence of lunar heat on relative humidity is negligible (Namias, 1951).

Fig. 8. Ambient temperature and general activity of coyote A recorded from 2200 to 0300 hours (hourly values, and pooling the values from each temperature group with the adjacent groups) over the period July 22, 1967 to June 2, 1968.


HOURS RECORDED
5 11 12 12 18 29 30 32 34 52 72 114 161 205 252 348 410 426 377 354 314 270 196 132 64 23 6
ACTIVITY (stereotyped turns) PER HOUR
10
20
30
40
50
STANDARD ERROR
MEAN
32-35 24-27 16-19 8-11 0-3 5-8 13-16 21-24 29-32 37-40 45-48 53-56 61-64 69-72
NEGATIVE
POSITIVE
AMBIENT TEMPERATURE (°F)

The data obtained indicate increasing activity with decreasing relative humidity (Fig. 9). This statistically significant association is contrary to the data presented by Orr (1959) for white-footed mice. I do not know the functional significance of this inverse relationship.

Activity and Barometric Pressure

The influence of barometric pressure on the activity of animals has long been known. Lombard (1892, cited by Brown et al., 1957) found that humans had an increased capacity for work at higher pressures than at low, and Hodge (1897, cited by Brown et al., 1957) noted a positive correlation between mean daily activity of two dogs and mean daily barometric pressure. Stewart (1898, cited by Brown et al., 1957) found a negative correlation between activity of gray rats and barometric pressure, while a positive correlation occurred when white rats were used. He concluded that the activity of wild animals displays a negative correlation, and that of domesticated animals displays a positive correlation with barometric pressure.

To determine whether there was a correlation between general activity of coyotes in captivity and barometric pressure, readings obtained between 2200 and 0300 hours were utilized. The resultant data (Fig. 10) suggest two possibilities. First, coyote A could have a critical "threshold" in the influence of barometric pressure on activity. This threshold appears to be 924.0 millibars, for pressures greater

Fig. 9. Relative humidity and general activity of coyote A recorded from 2200 to 0300 hours (hourly values, and pooling the values from each relative humidity group with the adjacent groups) over the period July 22, 1967 to June 2, 1968.

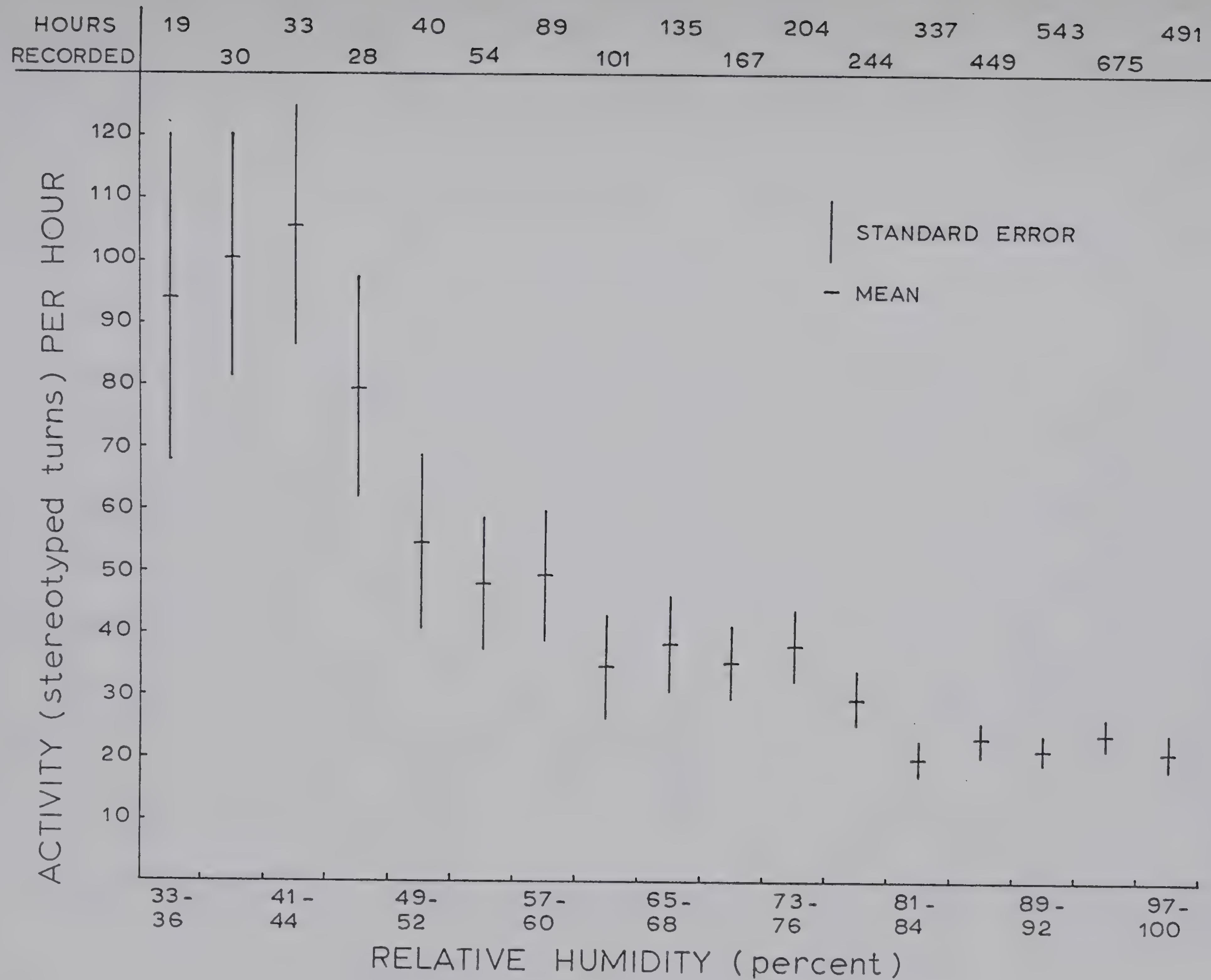
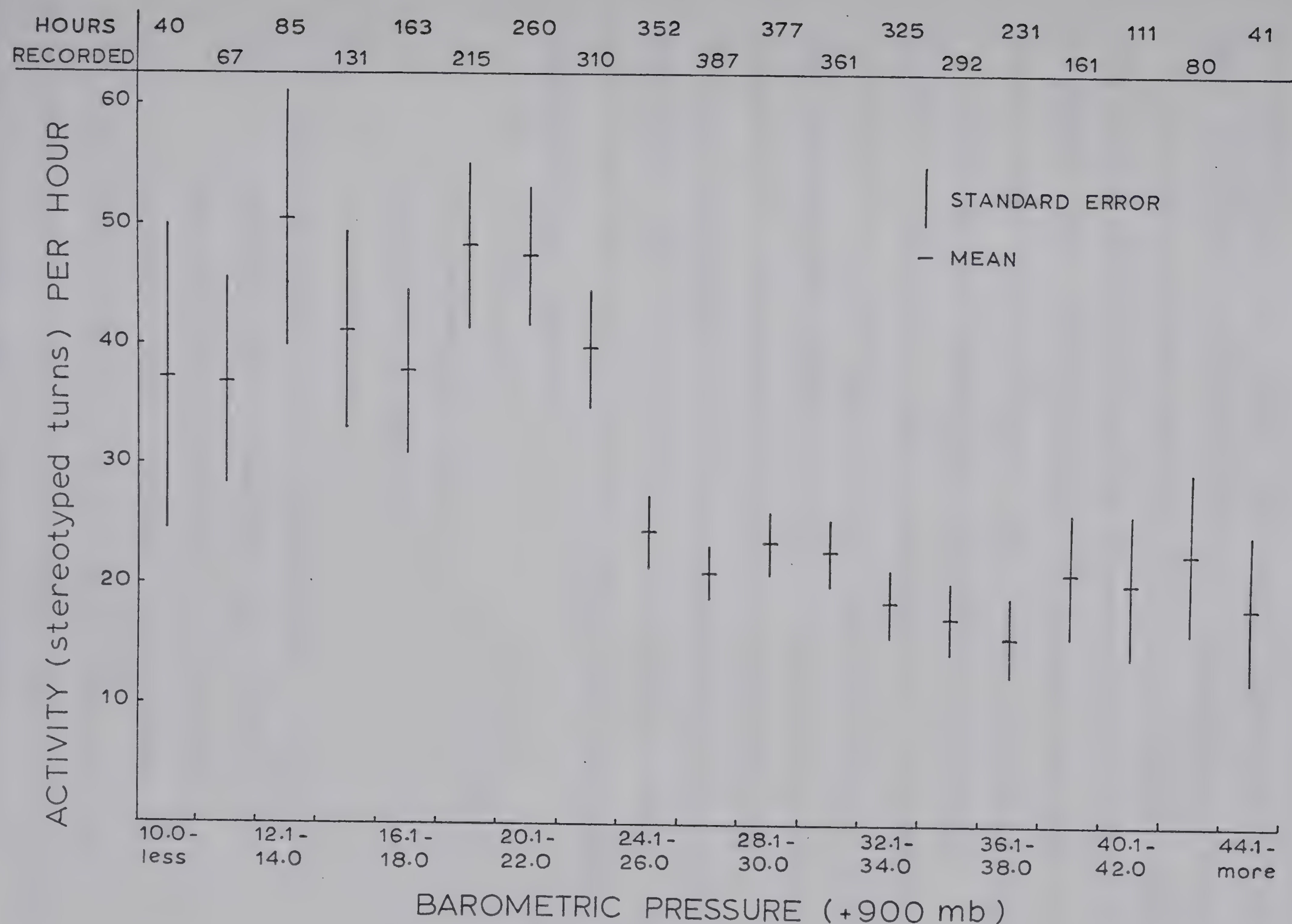

HOURS RECORDED
19
30
33
28
40
54
89
101
135
167
204
244
337
449
543
675
491
STANDARD ERROR
MEAN
ACTIVITY (stereotyped turns) PER HOUR
120
110
100
90
80
70
60
50
40
30
20
10
33-36
41-44
49-52
57-60
65-68
73-76
81-84
89-92
97-100
RELATIVE HUMIDITY (percent)

Fig. 10. Barometric pressure and general activity of coyote A recorded from 2200 to 0300 hours (hourly values, and pooling the values from each barometric pressure group with the adjacent groups) over the period July 22, 1967 to June 2, 1968.



HOURS RECORDED
40
67
85
131
163
215
260
310
352
387
377
361
325
292
231
161
111
80
41
STANDARD ERROR
MEAN
ACTIVITY (stereotyped turns) PER HOUR
60
50
40
30
20
10
10.0- less
12.1- 14.0
16.1- 18.0
20.1- 22.0
24.1- 26.0
28.1- 30.0
32.1- 34.0
36.1- 38.0
40.1- 42.0
44.1- more
BAROMETRIC PRESSURE (+900 mb)

than this result in decreased activity to a relatively constant level, and vice-versa. The second possibility is that there is a direct relationship between pressure and activity. I will assume the latter for this thesis, since the correlation between barometric pressure and activity is significant (-0.8208). This negative correlation supports the work of Stewart (1898, cited by Brown et al., 1957) mentioned above.

When the data on ambient temperature were grouped according to barometric pressure (Appendix 4), a significant correlation of -0.8579 was obtained. When the data on relative humidity were grouped according to barometric pressure (Appendix 5), a significant correlation of +0.7621 was obtained. To determine which factor (barometric pressure, temperature, or relative humidity) exhibited the closest association with general activity, the partial correlation coefficients were computed.

Let: 1 = activity

2 = barometric pressure

3 = relative humidity

4 = temperature

Then, the resultant coefficients are:

Holding 3 and 4 constant, $r_{12} = -0.7285$

Holding 2 and 4 constant, $r_{13} = -0.3572$

Holding 2 and 3 constant, $r_{14} = -0.6101$

The only significant correlation in these data are between activity and barometric pressure, suggesting a close association between general activity of coyote A and

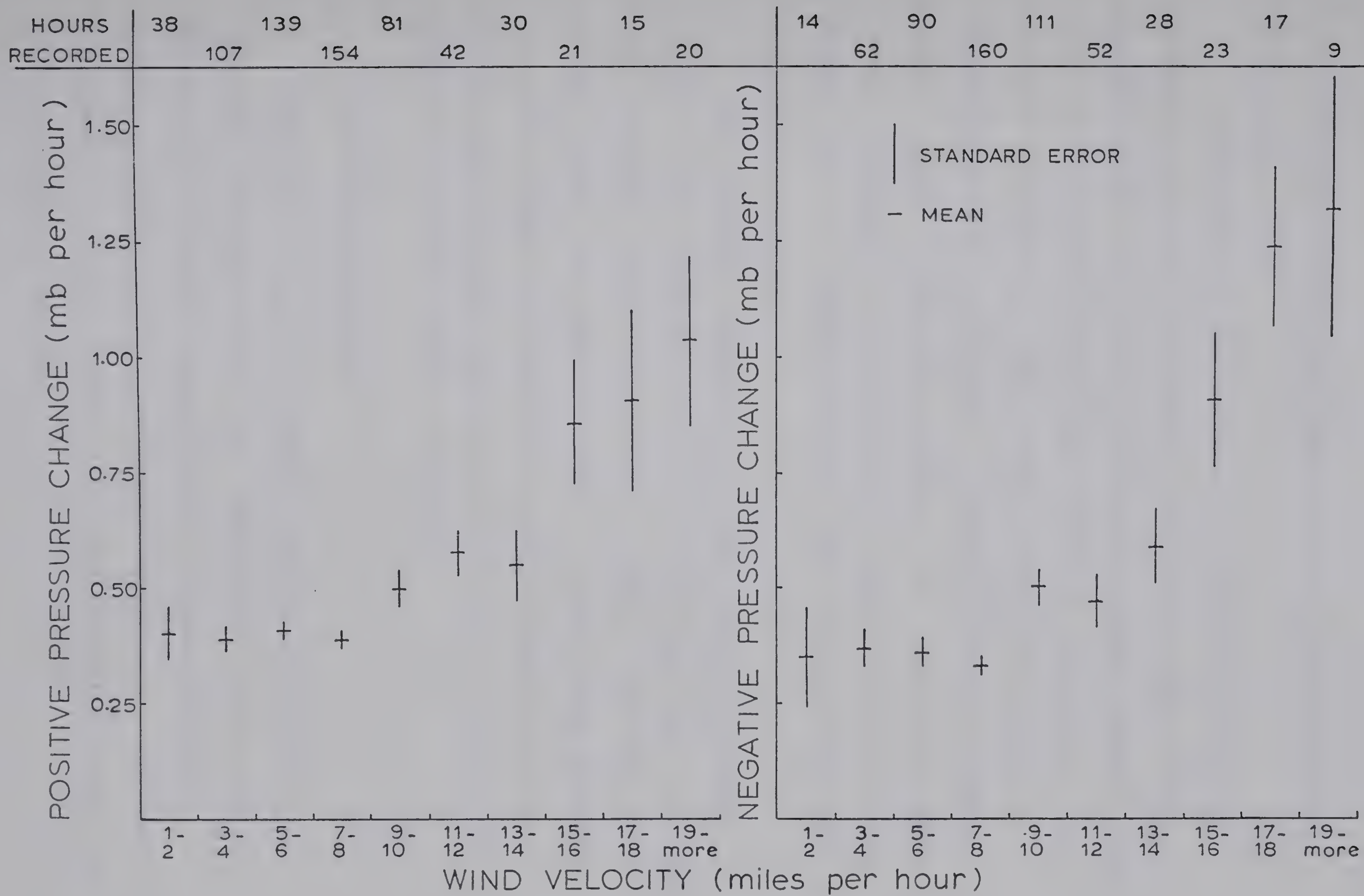
barometric pressure.

Activity and Wind Velocity

The effect of wind on general activity of coyotes in captivity could involve many factors. It is possible that wind could induce, or reduce activity by introducing olfactory and/or auditory elements. The wind could also influence activity by moving elements of the environment which the coyotes could see, or by influencing the physical comfort of the animal. However, I will consider wind as a simple meteorological element for this thesis. I hope to accomplish this by restricting this study to the association between wind velocity and change in barometric pressure, with the resultant influence on activity. I chose change in pressure because it is associated with the wind (Petterssen, 1958), and because barometric pressure exhibited the best relationship with the activity of coyote A (see "Activity and Barometric Pressure").

The association between magnitude of pressure change and wind velocity (Fig. 11) was independent of the direction of pressure change. This suggests that a specific wind velocity is generally indicative of a specific pressure change. Wind speeds up to 8 miles per hour are associated with a relatively constant pressure change of approximately 0.4 millibars per hour. Wind speeds up to 14 miles per hour are associated with a change in barometric pressure of appeoximately 0.5 millibars per hour. Winds greater than 14 miles per hour are associated with a rapid change in barometric

Fig. 11. Wind velocity and change in barometric pressure recorded from 2200 to 0300 hours (hourly values) over the period July 22, 1967 to June 2, 1968.



HOURS RECORDED
38
107
139
154
81
42
30
21
15
20
14
62
90
160
111
52
28
23
17
9
POSITIVE PRESSURE CHANGE (mb per hour)
1.50
1.25
1.00
0.75
0.50
0.25
NEGATIVE PRESSURE CHANGE (mb per hour)
STANDARD ERROR
MEAN
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-16
17-18
19-more
WIND VELOCITY (miles per hour)

pressure, and are probably indicative of a weather front (Petterssen, 1958).

An analysis of the relationship between a changing barometric pressure and general activity is shown in Fig. 12. Statistically, there is no difference between activity associated with a rising pressure and a falling pressure of less than 0.6 millibars per hour, with activity increasing as change in pressure increases. A greater pressure change, however, tends to decrease activity. For a positive pressure change in excess of 0.6 millibars per hour, the decrease is slight, but for a negative change, there is a statistically significant decrease.

This analysis suggests that small pressure changes associated with wind speeds up to 14 miles per hour may stimulate activity, while large pressure changes associated with weather fronts may reduce activity. A front which involves a positive change in barometric pressure appears to have a smaller dampening influence on activity than a front which involves a negative change in pressure.

Activity and Season

Seasonal changes in general activity of coyote A in captivity are shown in Fig. 13. These data indicate that the levels of activity during summer, autumn, and winter exhibit no statistically significant difference. The level of activity in spring, however, is significantly greater than during the rest of the year.

Fig. 12. Change in barometric pressure and general activity of coyote A recorded from 2200 to 0300 hours (hourly) values) over the period July 22, 1967 to June 2, 1968.

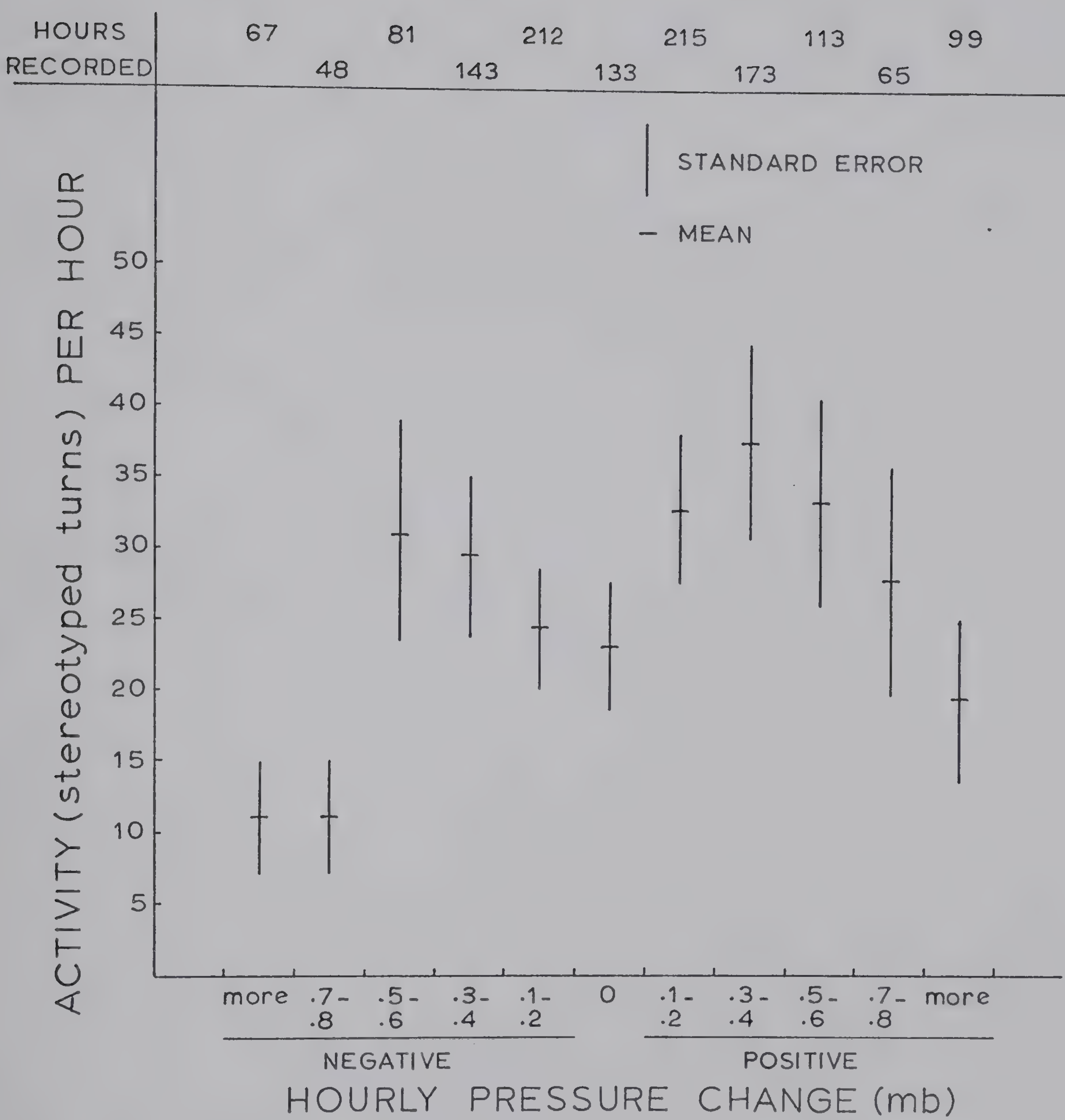
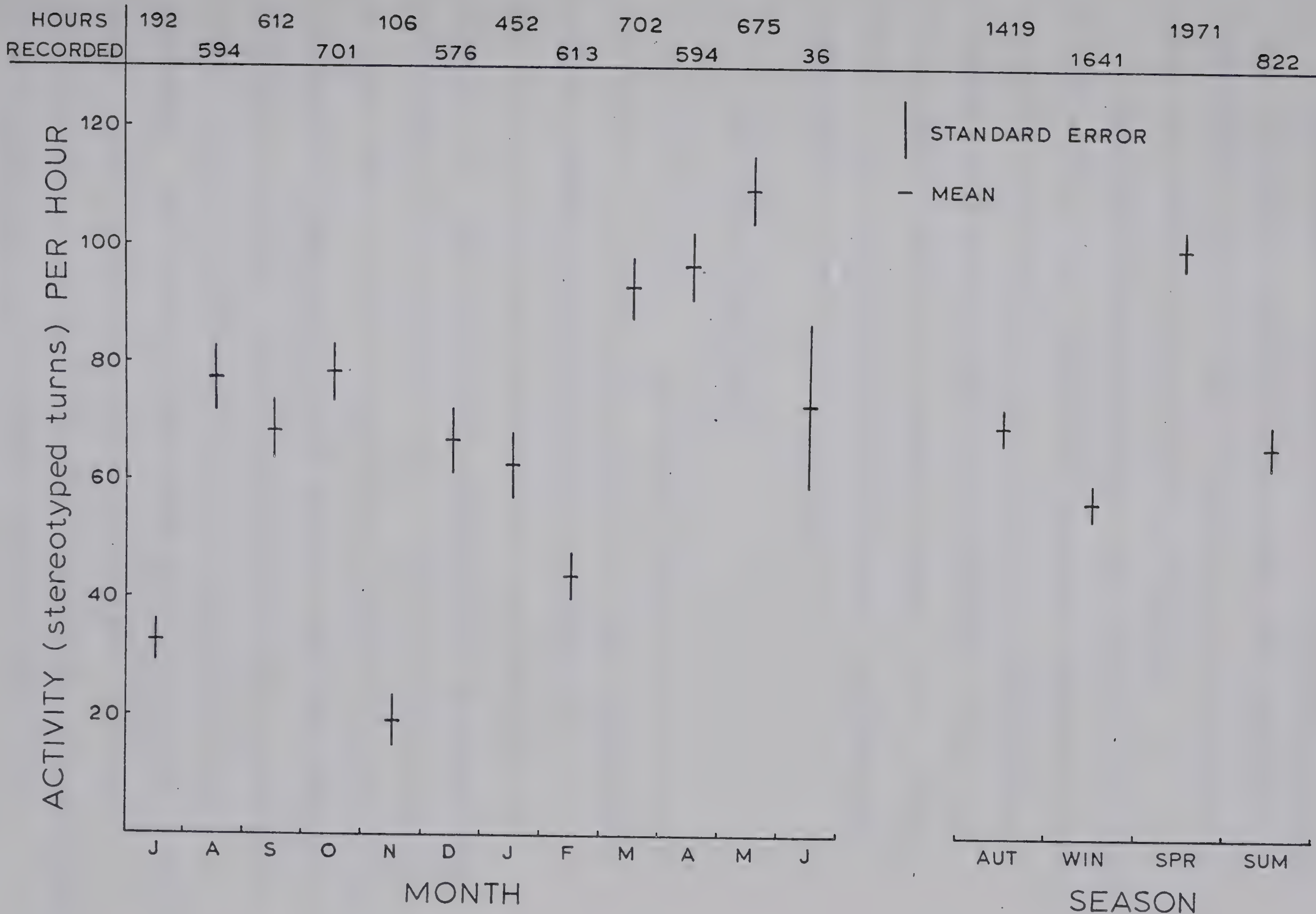

HOURS RECORDED
67
48
81
143
212
133
215
173
113
65
99
STANDARD ERROR
MEAN
ACTIVITY (stereotyped turns) PER HOUR
50
45
40
35
30
25
20
15
10
5
more
.7- .8
.5- .6
.3- .4
.1- .2
0
.1- .2
.3- .4
.5- .6
.7- .8
more
NEGATIVE
POSITIVE
HOURLY PRESSURE CHANGE (mb)

Fig. 13. Mean hourly activity of coyote A recorded during each month and season over the period July 22, 1967 to June 2, 1968.



HOURS RECORDED
192
594
612
701
106
576
452
613
702
594
675
36
1419
1641
1971
822
STANDARD ERROR
MEAN
ACTIVITY (stereotyped turns) PER HOUR
120
100
80
60
40
20
J A S O N D J F M A M J
MONTH
AUT WIN SPR SUM
SEASON

The changes in activity were plotted against monthly means of activity, barometric pressure, and temperature (Appendix 6) in an attempt to identify a causal factor. There was, however, no correlation exhibited.

One possible explanation for the increase in activity during spring could involve the behavioral characteristic of preparing dens for whelping. In "nature", unfertilized females not travelling with a mate sometimes prepare dens (Van Wormer, 1964), so it appears possible that a captive female could also be stimulated to prepare for whelping, resulting in an increase in activity.

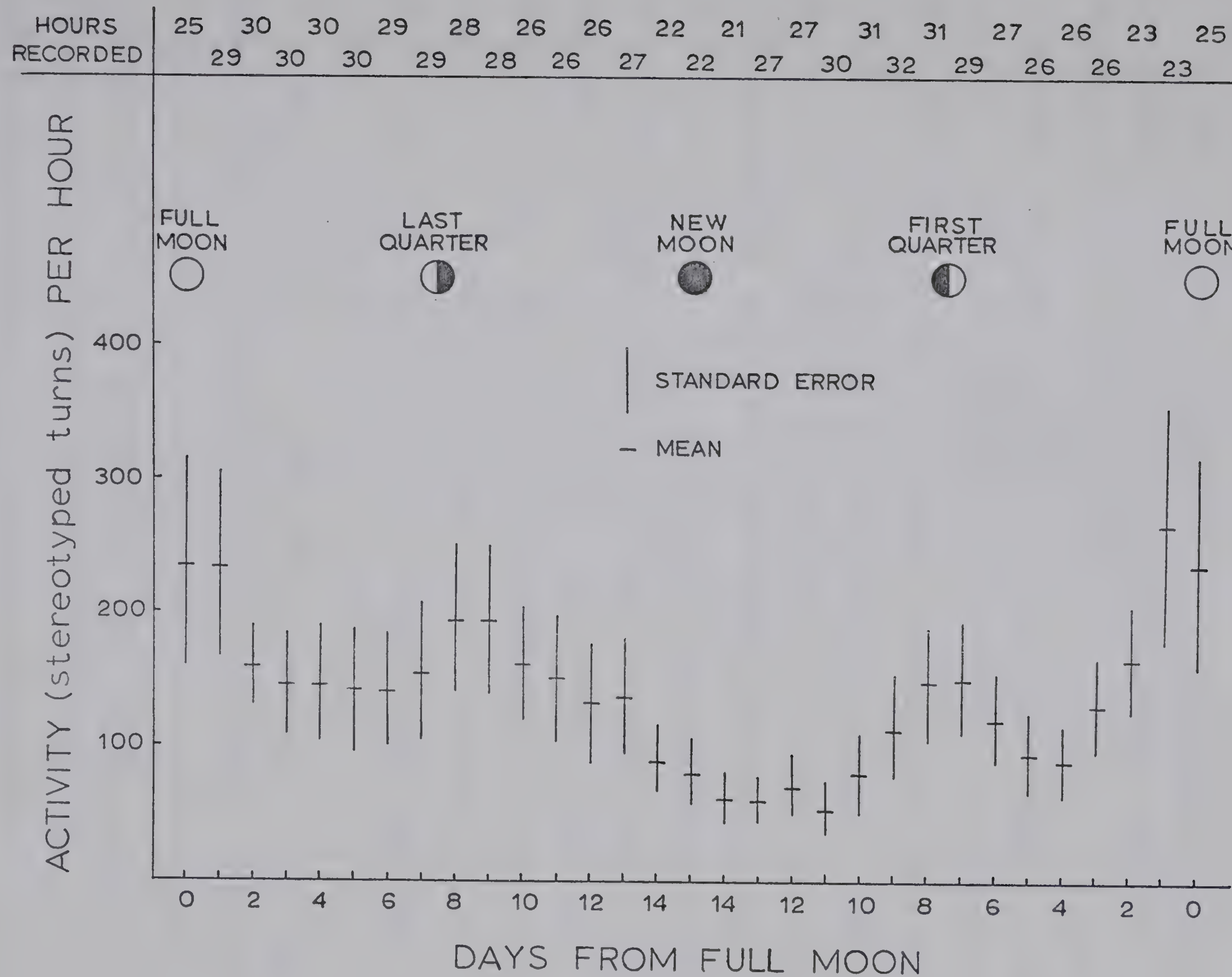
Activity and the Moon

The influence of the moon on coyote activity has held a prominent position in the folklore of these animals for several hundred years (Dobie, 1961), although little scientific evidence has been presented that supports this possibility. Several authors, however, have presented data that associate various behavioral patterns of other animals with the lunar cycle. An increase in general activity of the capercaillie (*Tetrao urogallus*) during a full moon has been reported by Siivonen and Koskimies (1955), while Brown et al. (1956) state that molluscs open their shells more during a full moon. The Pacific palolo worms (*Eunice viridis*) reproduce seven, eight, or nine days after the November full moon (Corney, 1922, cited by Jolly, 1966), while the Atlantic palolo worms (*Leodice fucata*) reproduce eight days after the

July full moon (Clark and Hess, 1942, cited by Jolly, 1966). The grunion (*Leuresthes tenuis*) spawns during the spring tides which occur from March through August (Walker, 1952), while Harrison (1954, cited by Cowgill et al., 1962) reported that Selangor rats breed more often just before a full moon. Evidence of a close association between a full moon and the reproductive season has been reported by Cowgill et al. (1962) for the black lemur (*Lemur macaco*), and by Jolly (1966) for the ringtailed lemur (*L. catta*). Dewan (1968) has even demonstrated a possible association between the light of the full moon and the menstral cycle of humans. However, no reference was found that related gross activity of mammals with the lunar cycle. It is the purpose of this section to test for an association between the lunar cycle and general activity of coyotes in captivity.

Data accumulated between 2300 and 0100 hours over the period July, 1967 to June, 1968 (Fig. 14) suggest that activity is associated with the lunar cycle. A plot of the high activity exhibited during the full moon, and the low activity during the new moon, takes the form of a modified sine curve. An hypothesis will be presented in the concluding discussion which might explain this apparent oscillation in general activity of coyotes in captivity during the lunar cycle.

Fig. 14. Lunar cycle and general activity of coyote A recorded from 2300 to 0100 hours (hourly values, and pooling the values from each lunar day with the adjacent days) over the period July 22, 1967 to June 2, 1968.



HOURS RECORDED
25 29 30 30 30 30 29 29 28 28 26 26 26 27 22 22 21 27 27 30 31 32 31 29 27 26 26 26 23 23 25
FULL MOON
LAST QUARTER
NEW MOON
FIRST QUARTER
FULL MOON
STANDARD ERROR
MEAN
ACTIVITY (stereotyped turns) PER HOUR
400
300
200
100
0 2 4 6 8 10 12 14 14 12 10 8 6 4 2 0
DAYS FROM FULL MOON

Environmental Factors and the Bed Site

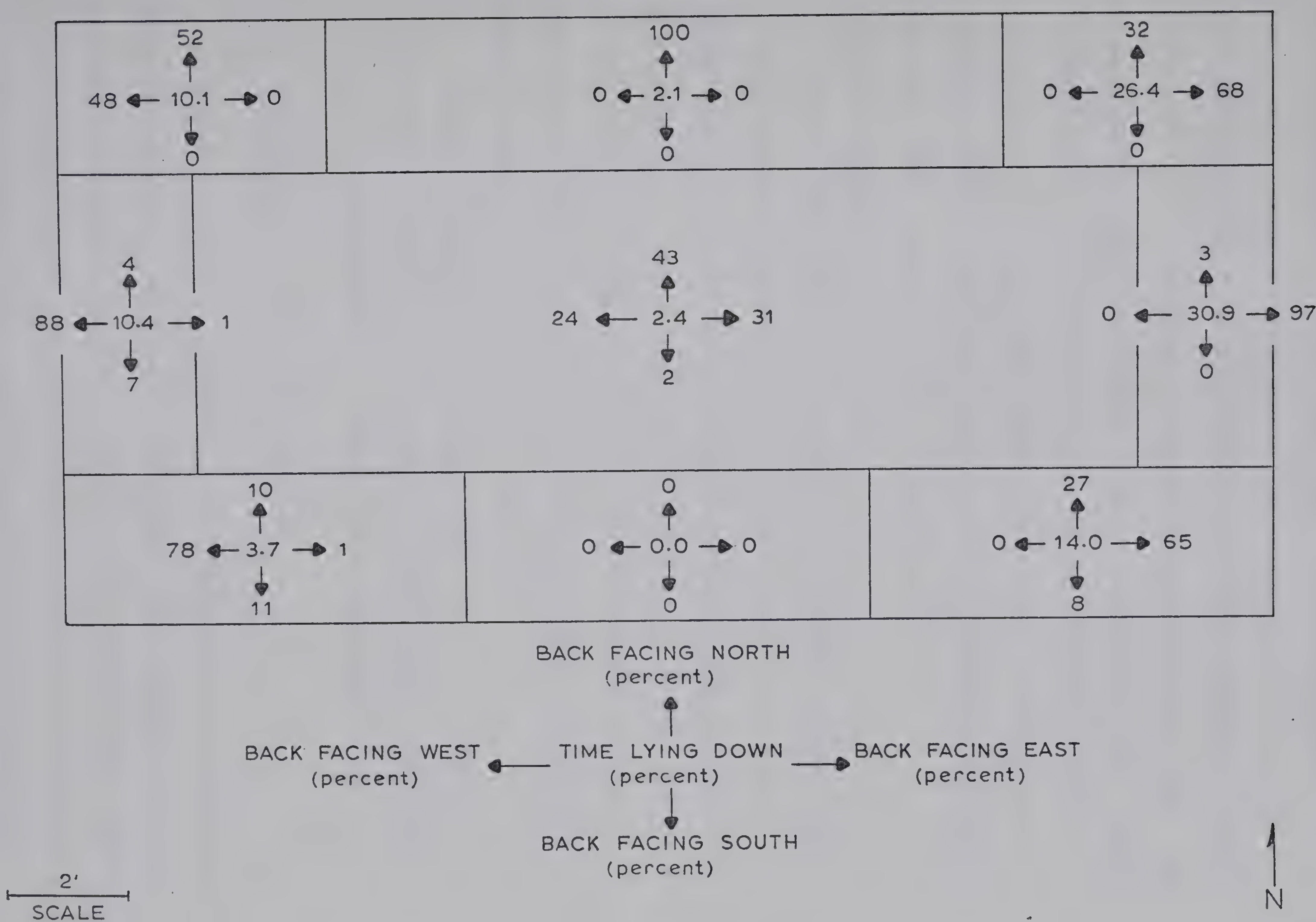
Locations Utilized When Lying Down

In an attempt to determine if captive coyotes exhibit a consistency in the location of their bedding sites, the locations utilized in cage 3 (Fig. 4) by coyotes D, E and F when lying down were recorded. The data were pooled to determine if the structure of the cage influenced the bedding sites of a population of captive coyotes. Variation between the animals, and social implications were not analysed. The time spent in the shelter was omitted, because the utilization of this site generally occurred when the animals were "frightened".

The resultant data (Appendix 7), when grouped according to the orientation of the animals and the time spent at each location, show nine "zones" which were utilized when lying down (Fig. 15). The intensity of utilization of these zones suggests that bedding sites were located primarily at the ends of the cage, and toward the corners of the cage away from the south side, which was visually open.

The preference for lying down at the ends of the cage could be attributed to the structure of the cage. Since the cage was rectangular, a running animal would travel along the long axis and turn at the ends. The turning moved the substrate (snow or straw) toward the ends of the cage, resulting in an increase in elevation of approximately six inches over the central portion of the cage. Since coyotes prefer a slightly elevated spot for a bedding site in nature

Fig. 15. Location of bed and orientation of the body exhibited by coyotes D, E and F when lying down in cage 3.


52
48
10.1
0
0
100
0
2.1
0
0
32
0
26.4
68
0
4
88
10.4
1
7
43
24
2.4
31
2
3
0
30.9
97
0
10
78
3.7
1
11
0
0
0.0
0
0
27
0
14.0
65
8
BACK FACING NORTH
(percent)
BACK FACING WEST
(percent)
TIME LYING DOWN
(percent)
BACK FACING EAST
(percent)
BACK FACING SOUTH
(percent)
2′
SCALE
N

(Ozoga and Harger, 1966), this could also be involved in captivity. However, the north and south sides of cage 3, although exhibiting equal elevation of the substrate, were utilized as a bed site to a different degree (Fig. 15). The animals spent more time lying down by the north wall, which was wood, than by the south wall, which was wire. This trait could be associated with an element of "security", since the directions the animal could be approached from are reduced. This concept will be examined further in "Orientation When Lying Down".

The trend toward utilizing the east end of the cage as a bed site more than the west end may indicate that the animals tend to locate their bed away from the gate of the cage. However, I believe that utilization of the east end of the cage as a bed site has an element of concealment associated with it, since the animal would be hidden from a person located at the vivarium (Fig. 1).

The possibility that lying next to a wall provides protection or comfort in relation to the weather will be covered in "Meteorological Factors and the Bed Site".

Orientation When Lying Down

When coyotes D, E and F were lying down, the direction that the back of the animal faced and the direction of curling (clockwise or counterclockwise) were recorded at the various locations utilized in cage 3 (Fig. 4). The resultant data (Appendix 7; Fig. 15) indicate that the animals located

themselves next to a wall with their backs toward the wall 86 percent of the time.

Lying with the back to the walls of the cage could be explained as "security seeking" behavior, because when lying in this position, the directions from which enemies could approach are reduced. This trait could also involve visual "curiosity" since the head of the animal is directed toward the open sides of the environment, thus facilitating visual observation.

The total time of clockwise versus counterclockwise lying, at the level of the individual (Table 1), suggests that the direction of curling is not random. Coyote D appeared to have no favored side, while coyote E spent 67.7 percent of the time lying down on its right side, and coyote F spent 66.9 percent of the time lying down on its left side. Statistically, both coyotes E and F displayed asymmetry in the direction of curling.

It is possible that the asymmetrical direction of curling exhibited by coyotes E and F resulted from a stereotypic approach-path to the bed. Thus, if coyote F consistently approached a bed site along a clockwise path, the direction of curling would tend to be clockwise. However, I do not believe that this was involved, since the pattern between walking and lying down was generally discontinuous, thus losing the momentum of the approach to the bed.

A more probable explanation would involve the skeletal systems of the animals. Jolicoeur (1963), studying marten (*Martes americana*), found a significant predominance in the

Table 1. Frequency of clockwise versus counterclockwise orientation when lying, exhibited by coyotes D, E and F.

	Direction of Curling				
	Clockwise		Counterclockwise		
Coyote	Minutes	%	Minutes	%	Total
D	2337	47.6	2574	52.4	4911
E	703	32.3	1473	67.7	2176
F	1694	66.9	838	33.1	2532
Total	4734	49.2	4885	50.8	9619

length of the right humerus. He suggests that this increase in length may be related to the frequency or way in which the right and left forelimbs are used. If this conclusion is valid for coyotes, then coyotes D, E and F could be classed as ambidextrous, dextral, and sinistral individuals, respectively. An increase in length of one humerus could explain the non-randomness of the direction of curling, since an animal with a long limb on one side would tend to travel toward the opposite side. This would suggest that the humeri of coyote D are equal in length, while coyote E has a right humerus that is longer than the left, and vice versa for coyote F. The lengths of the humeri, however, were not measured.

Meteorological Factors and the Bed Site

The possible association between ambient temperature, sunshine, and time of day on the spatial utilization of cage 3 was examined by utilizing the periods of inactivity of coyote D. This animal was chosen because it was the dominant animal and should have been the least affected by the locations of its litter mates. Only the time spent at the west end (1a to 4a) or east end (9c to 12c) of cage 3 (Fig. 4) was used, since the maximum protection, or exposure, from the sun was obtained at these locations.

The resultant data (Table 2) appear to present certain trends. The data suggest that when the weather was cold and cloudy, there was no association between the bed site and

Table 2. Ambient temperature and cloud cover in relation to the bed site of coyote D.

Time of Day	Temperature (^{o}F) Less Than 40 (Cold)	Temperature (^{o}F) More Than 40 (Warm)	Sunshine (% Per Hour) Less Than 50 (Cloudy)	Sunshine (% Per Hour) More Than 50 (Sunny)	Lying Down Location (Minutes) Sun	Lying Down Location (Minutes) Shade	Percent of Time in Sun
	X		X		96	203	32.1
	X			X	273	305	47.2
Morning		X	X		59	7	89.4
		X		X	7	985	0.7
							42.4
	X		X		198	122	61.8
	X			X	321	78	80.5
Afternoon		X	X		506	60	89.4
		X		X	741	448	62.3
							73.5
	X		X		294	325	47.5
	X			X	594	383	60.8
Daily		X	X		565	67	89.4
		X		X	748	1433	34.3
							58.0

the location of the sun. However, on cold, sunny days and warm cloudy days, there was a trend toward lying in the sun, while on warm, sunny days the trend was toward lying in the shade.

The possible influence of wind on the utilization of cage 3 was examined by summing the periods of inactivity of coyote D at cage locations 1a to 5a and 5c, 9c to 12c (Fig. 4) in relation to the wind. The data (Table 3) suggest a trend for coyote D to utilize the end of the cage from which direction the wind was blowing. This trend would suggest that the animal seeks the protection of the cage wall.

Since no significant association was found between the bed site of coyote D and the meteorological elements examined, it appears that the structural characteristics of the cage are the primary factors involved in the localization of the bed. This aspect was covered under "Locations Utilized When Lying Down". The data presented above suggest that the micro-climate is of secondary importance in locating a bed site.

Behavior Associated With Lying Down

Sniffing the Ground Before Lying Down

Berlyne (1960) reported that the first minute or two of exposure to a situation is the period when exploration has a special role. A measure of this "perceptual exploration" (Berlyne, 1960) in captive coyotes was obtained by recording the occurrence of olfactory investigation of the bed site prior to lying down (Appendix 8).

Table 3. Wind direction and the bed site of coyote D.

Wind Direction	Location of Bed Site: West End of Cage (1a-5a) Minutes	%	East End of Cage (5c, 9c-12c) Minutes	%	Total Time (Minutes)
NE E SE	138	29.0	338	71.0	476
SW W NW	613	33.7	1206	66.3	1819
Total	751	32.7	1544	67.3	2295

The resultant data (Table 4) indicate that investigation of the bed site occurs 79 percent of the time, with no significant individual variation. Although this suggests that there were no social implications in this behavioral pattern, I believe that the reduced frequency of investigative sniffing exhibited by the beta animal (coyote F) could be associated with its social rank. It is possible that olfactory investigation could be of secondary importance for this animal, and that it could be locating its bed in relation to the dominant animal. Insufficient data, however, does not permit this analysis.

Turning Around Before Lying Down

Turning around before lying down is well known in canids, but the functional significance, if any, of this behavioral pattern is not clear. Scott and Fuller (1965, p. 74) believe that it "has the adaptive function of feeling with the paws for a smooth area on which to rest." Scott (1967, p. 380) also remarked that this pattern "has been imaginatively interpreted as tramping down grass or snow", but he emphasized that both are nothing more than "enlightened guesses."

During this study, I recorded the presence or absence of this pattern as exhibited by coyotes D, E and F (Appendix 8). The 645 times that these animals were observed lying down was insufficient for any individual analysis, but the resultant data (Table 5) do present some trends for the litter.

Table 4. Investigation of the bed site exhibited by coyotes D, E and F before lying down.

Coyote	Number of Times Lying Down (percent in brackets) No Exploratory Sniffing		Sniffing the Bed		Total	
D	49	(19.3)	205	(80.8)	254	(100.0)
E	32	(20.8)	122	(79.2)	154	(100.0)
F	28	(23.3)	92	(76.7)	120	(100.0)
Total	109	(20.6)	419	(79.4)	528	(100.0)

Tabe 5. Frequency of turning around before lying down exhibited by coyotes D, E and F during various seasons and temperatures.

Month	Temperature (^{o}F)	Times Observed Lying Down No Turning	Times Observed Lying Down Turning	Lying Down With Turning (Percent)
December	19 - less	16	48	75.0
January	20 - 29	32	28	46.7
February	30 - more	23	25	52.1
March	19 - less	4	8	66.7
April	20 - 29	12	5	29.4
May	30 - more	328	116	26.1
	19 - less	20	56	73.7
	20 - 29	44	33	42.9
	30 - 39	120	67	35.8
Total	40 - 49	58	34	37.0
	50 - 59	117	21	15.2
	60 - more	56	19	25.3

When ambient temperature was compared with the percentage of times that lying down involved turning around, a significant correlation of -0.8689 was obtained. This suggests an increase in the occurrence of the turning pattern at lower temperatures. If this is true, it would appear that captive coyotes do not turn around solely for the purpose of finding a smooth bed (Scott and Fuller, 1965), although this function could be involved. The association between temperature and turning will be discussed further under "Postures Utilized When Lying Down".

When the frequency of the turning pattern at various temperatures during winter months was compared with the frequencies exhibited during spring months (Table 5), there was no statistical difference.

The possibility that turning around has the function of "tramping down grass or snow" (Scott, 1967) seems to be occasionally involved. Of the 645 times the animals were observed lying down, turning around was exhibited 230 times (Table 5), of which a definite "tramping" was observed 5 times. While the typical turning was a "passive" action, these "tramping" patterns consisted of actively thrusting the feet downward, an action which was highly suggestive of preparing a bed.

The 475 turning patterns observed (includes turning before sitting) consisted of 447 complete turns. This resulted in an average of 0.94 turns per event. The direction of turning was arbitrary, since the difference between the

number of clockwise turns (217), and the number of counter-clockwise turns (230) was insignificant.

Pawing the Ground Before Lying Down

Murie (1940) observed wolves digging a bed in the dirt, a pattern which is occasionally seen in domestic dogs (R. P. Stoneberg, pers. comm.). During this study, I observed this pattern in 50 of the 645 times that the coyotes were observed lying down (Appendix 8).

Pawing the ground before lying down was exhibited in 6.0 percent of the "walk to lying" patterns, while pawing occurred in only 2.4 percent of the "lying to standing to lying" patterns. These data are statistically different, and suggest that pawing is associated with preparing a bed by making the ground smooth. The low frequency of pawing associated with the "lying to standing to lying" patterns suggest that a location that has been utilized as a bed is generally smoother than a new bed.

Postures Utilized When Lying Down

Regulation of body temperature during periods of inactivity is partially accomplished by the position of the animal. Hoar (1966) states that an uneven covering of fur with poorly insulated extremities serves as an avenue of heat dissipation. This infers that if an animal's legs are poorly insulated, an animal which is lying on it's side with legs extended would lose more body heat to the environment than

an animal which is curled-up, assuming the physiology of the animal remains constant. It also implies that when ambient temperature is high, a more exposed prone position would be exhibited, and vice versa.

Three basic positions are adopted by coyotes when they lie down. During this study, these positions were designated as:

Lying Position 1 - Lying on side with both front and hind legs extended at right angles to the axis of the body, and the side of the muzzle on the ground (Fig. 16).

Lying Position 2 - Lying on side with both front and hind legs tucked under the trunk of the animal, and the muzzle flat on the ground and exposed (Fig. 17).

Lying Position 3 - As Lying Position 2, but muzzle tucked under the tail (Fig. 18).

The position utilized when lying down appears to be associated with ambient temperature (Table 6). Lying Position 1, which exhibits the maximum exposure of the poorly insulated extremities (Fig. 16) was rarely utilized in cold temperatures, but became the dominant pattern during hot temperatures. Lying Position 2, which exhibits a moderate exposure of the extremities (Fig. 17), was the dominant pattern during warm temperatures, while Lying Position 3, with the minimum of exposure (Fig. 18), was the prevalent pattern during cold weather.

Fig. 16. Coyote in "Lying Position 1".

Fig. 17. Coyote in "Lying Position 2".

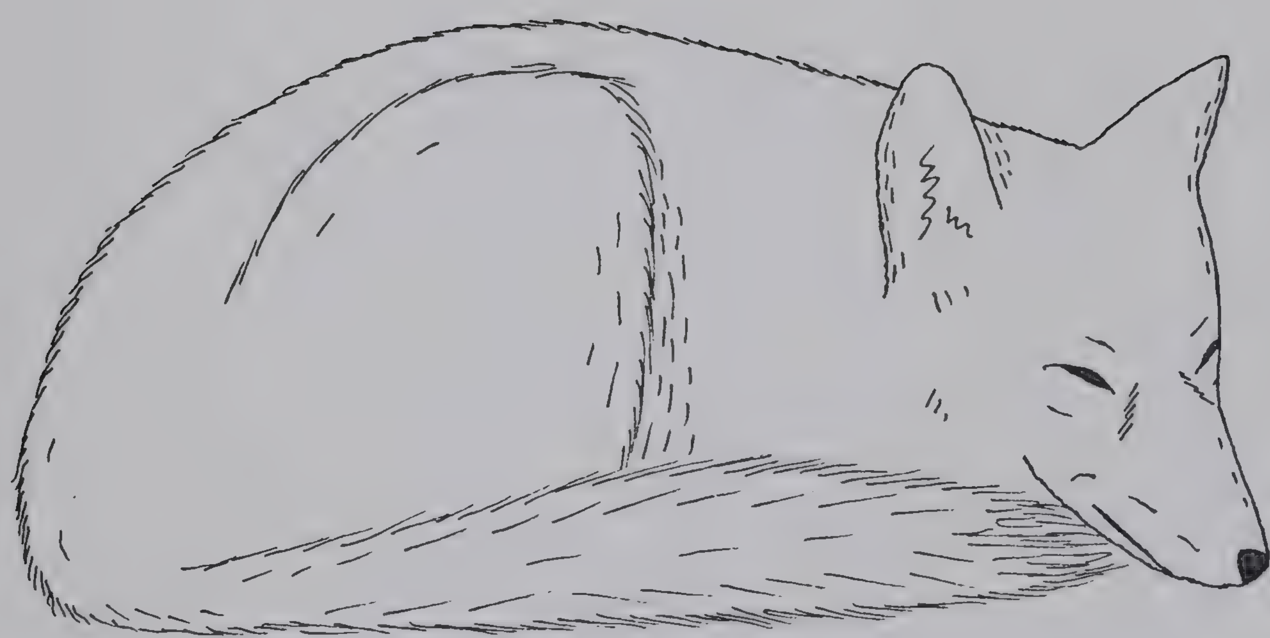


Fig. 18. Coyote in "Lying Position 3".

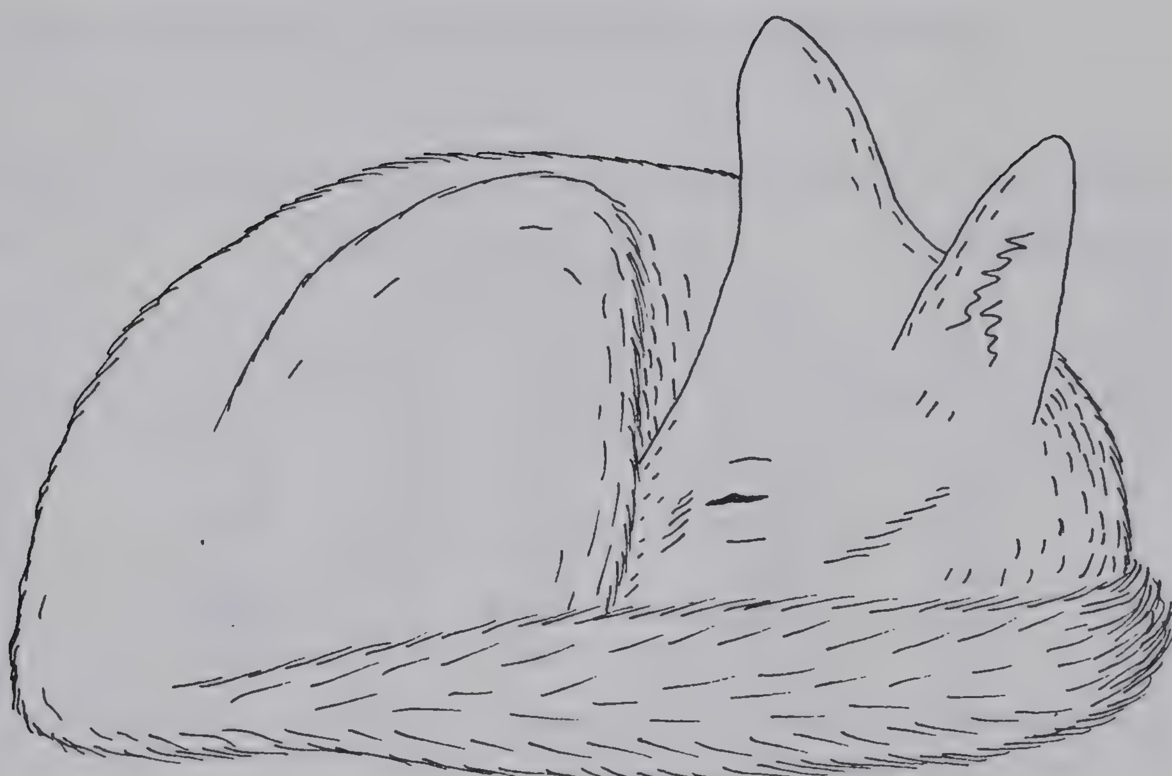


Table 6. Ambient temperature and body position utilized by coyotes D, E and F while lying down.

Temperature (^{o}F)	Time Lying Down (Minutes) L_1	L_2	L_3	Total	Time Lying Down (%) L_1	L_2	L_3
19 - Less	12	81	848	941	1	9	90
20 - 29	0	43	697	740	0	6	94
30 - 39	495	804	1262	2561	19	32	49
40 - 49	220	318	374	912	24	35	41
50 - 59	920	374	1094	2388	39	16	45
60 - More	526	163	87	776	68	21	11

Rutter and Pimlott (1968, p. 137) stated that "the curled-up position gives good protection from flies." The concept of "protection from flies" as a function of Lying Position 3 could explain the 11 percent value for temperatures which are greater than, or equal to, 60°F (Table 6).

There appears to be an association between the turning pattern (p. 45) and assumption of the curled-up posture. Although turning around may be a measure of the "reluctance" of the animals to come in contact with the ground when lying down, it is probably a preparatory pattern which orients the body for assuming a curled-up position.

Huddling At Low Temperatures

The behavioral pattern of huddling has been shown to be of considerable value as a survival mechanism in some small mammals (Sealander, 1952; Brody, 1945) and in certain species of birds (Gerstell, 1942). This phenomenon has also been documented for the muskox, *Ovibos moschatus* (Hamilton, 1939), while Allen and Mech (1963) reported that wolves sleep near each other for warmth.

The possibility of huddling at low temperatures in captive adult coyotes was examined by recording the time and temperature when any two animals were less than five feet apart during periods of inactivity (Table 7).

Statistically, these data are insignificant. This infers that huddling in the conditions of this study has no relationship with ambient temperature.

Table 7. Ambient temperature and huddling exhibited by coyotes D, E and F.

Temperature (°F)	Total Time of Inactivity (Minutes)	Total Time When Lying Less Than 5.0 Feet Apart (Minutes)	(%)
19 - Less	2024	1177	58
20 - 29	1053	396	38
30 - 39	3324	1251	38
40 - 49	1066	759	71
50 - 59	3849	2847	74
60 - More	1758	811	47

Leaving the Bed

Hoar (1966) states that increased muscle tone, like shivering, is a muscular response associated with heat production. He refers to this response as physical thermogenesis, and remarks that cooling of the body surfaces increases this reaction.

Since stretching appears to be an exaggerated form of increased muscle tone, it seems reasonable to assume that stretching after a period of inactivity would prepare the animal for "action", probably in part through increased heat production. It also appears logical to predict an increase in number and/or frequency of stretch-responses in colder weather.

The effect of temperature and season on post-inactivity behavior was examined by recording the arousal patterns of coyote D, E and F. This involved recording time of inactivity, occurrence of walking or stretching upon arousal, and type of stretch exhibited when it occurred.

Three basic types of stretch-responses were noted:

Stretch Position 1 - Front quarters lowered with front legs extended anteriorly; hind quarters raised with hind legs straight (Fig. 19).

Stretch Position 2 - Converse of Stretch Position 1 (Fig. 20).

Stretch Position 3 - Both front and hind quarters raised; back arched like a "spitting cat" (Fig. 21). This pattern could

Fig. 19. Coyote in "Stretch Position 1".

Fig. 20. Coyote in "Stretch Position 2".

Fig. 21. Coyote in "Stretch Position 3".

have a social function since it resembles the "challenging attitude" presented by Murie (1940).

The data on the behavioral patterns exhibited by coyotes D, E and F following a period of lying down (Table 8) suggest that certain trends are involved.

Immediate walking after lying down appears to be independent of temperature and season, but the lying down period associated with a walk-response appears to be shorter than those periods which result in a stretching pattern. This suggests that walking, after a period of inactivity, is the arousal-pattern exhibited when the time spent lying down is insufficient for the animal to "cool-off". However, the difference between the periods of lying down for temperatures above and below freezing appears to be too small. Because of this, I suggest that a walk-response could be indicative of an "interrupted" period of inactivity, and that walking is possibly a fear-response. My observations tend to support this possibility, since a "frightened" animal rarely exhibited a stretch-response.

Another trend appears when the average time the animals lay down for a "stretch-arousal" is compared with ambient temperature (Table 8). The data suggest that cold weather results in shorter periods of inactivity.

An analysis of variance of the number and type of stretch-responses (Table 9) gave a significant relationship between season and type of stretch exhibited. During winter

Table 8. Ambient temperature and season in relation to the behavioral patterns of coyotes D, E and F following a period of lying down.

Month	Temperature	Number Observed		Average Time Lying Down (Minutes)		Number of Stretches			Mean Stretches After Lying Down
		Stretch	Walk	Stretch	Walk	Str_1	Str_2	Str_3	
Winter*	Below 32	40	18	25.6	10.8	29	20	27	1.85
	Above 32	21	9	30.2	22.3	6	7	17	1.43
	Total	61	27	27.2	14.6	35	27	44	1.71
Spring**	Below 32	15	6	27.1	25.0	15	5	5	1.25
	Above 32	57	42	42.3	17.7	43	21	10	1.42
	Total	72	48	39.1	18.6	58	26	15	1.38
	Below 32	55	24	26.0	14.4	44	25	32	1.66
Total	Above 32	78	51	39.0	18.5	49	28	27	1.42
	Total	133	75	33.7	17.2	93	53	59	1.53

* Includes December, January, and February.
**Includes March, April, and May.

Table 9. Number and type of stretches exhibited by coyotes D, E and F in relation to temperature, season, and time lying down.

Stretch Type	Time Lying (Minutes)	Winter Below 32°F	Winter Above 32°F	Total	Spring Below 32°F	Spring Above 32°F	Total	Total Seasons Below 32°F	Total Seasons Above 32°F	Total
Str_1	1-30	0.62	0.33	0.95	0.91	0.67	1.58	1.53	1.00	2.53
	31-More	0.93	0.22	1.15	0.50	0.94	1.44	1.43	1.16	2.59
	Total	1.55	0.55	2.10	1.41	1.61	3.02	2.96	2.16	5.12
Str_2	1-30	0.46	0.33	0.79	0.09	0.33	0.42	0.55	0.66	1.21
	31-More	0.57	0.33	0.90	0.25	0.48	0.73	0.82	0.81	1.63
	Total	1.03	0.66	1.69	0.34	0.81	1.15	1.37	1.47	2.84
Str_3	1-30	0.38	0.75	1.13	0.09	0.13	0.22	0.47	0.88	1.35
	31-More	1.14	0.89	2.03	0.50	0.27	0.77	1.64	1.16	2.80
	Total	1.52	1.64	3.16	0.59	0.40	0.99	2.11	2.04	4.15
Total	1-30	1.46	1.41	2.87	1.09	1.13	2.22	2.55	2.54	5.09
	31-More	2.64	1.44	4.08	1.25	1.69	2.94	3.89	3.13	7.02
	Total	4.10	2.85	6.95	2.34	2.82	5.16	6.44	5.67	12.12

(December, January, and February), there was a significant shift away from Stretch Position 1 (Fig. 19) toward Stretch Position 3 (Fig. 21), while in spring (March, April, and May) the converse was true. Stretch Position 2 (Fig. 20) remained at a constant rate of occurrence during both seasons.

This shift in stretch-type may be associated with the reproductive period. Since coyotes in Alberta mate in late February (Soper, 1964), the winter sample would include the preparatory period (pro-oestrum) and the mating period (Whiteman, 1940). If Stretch Position 3 (Fig. 21) is associated with the "challenging attitude" of Murie (1940), the increase in number during the reproductive season could indicate a greater frequency of interactions between the animals. Scott and Fuller (1965) remark that the reproductive period causes domestic dogs to become highly "excited", suggesting a greater number of interactions.

There is an interesting trend in the number and type of stretch-response (Table 9) which suggests a greater number of stretches with an increased period of lying down. This implies that stretching may function as a warming-up mechanism to facilitate muscular and/or nervous responses.

Behavior Associated With Self-Grooming

Scratching and Biting

Scott and Fuller (1965) reported that domestic dogs will scratch or nip an "irritating" region, but they did not mention the relative frequency of each pattern, or the body

region which receives each response.

During this study, I recorded scratching and biting involved in self-grooming exhibited by coyotes D, E and F. Scratching or biting as a displacement activity (Hinde, 1966) was never detected with coyotes D, E and F, although coyote A, on one occasion, exhibited what appeared to be displacement biting. This displacement activity occurred when coyotes D, E and F were playing in cage 3 (Fig. 1). Coyote A, in cage 1, became highly "excited", and whirled around in a circle while biting her flank. It is possible that the "excitement" of the play in the adjacent cage may have promoted certain autonomic activities which, in turn, elicited biting (Hinde, 1966). However, it is also possible that this apparent displacement activity was actually a response to an irritation. In any case, it appears that scratching or biting as a displacement activity was rarely, if at all, exhibited by these coyotes.

Morphological characteristics appear to influence which response is exhibited. Scratching was directed only toward the head, neck, and shoulder, while the rest of the body and the shoulder received a bite-response. The primary region which received scratching was the lower half of the head (43.8 percent). Biting was directed mainly toward the thoracic region of the back (40.0 percent).

Although scratching was exhibited 51.6 percent of the time, it was directed toward approximately 1/5 (an estimate of the body. This represents a significantly greater frequency

of responses in the head-neck region than for the rest of the body. If scratching and biting are a means of relieving an irritation, this concentration could indicate that biting is more effective, if the irritation is evenly distributed over the body. However, the concentration of bite-responses in the thoracic region of the back suggests that the causal factor, if any, which elicits scratching or biting is concentrated toward the anterior portion of the animal. This suggests that scratching and biting are probably equal in effectiveness for relieving an irritation, and that the response which is exhibited depends on the location of the irritant.

Licking

Scott and Fuller (1965) report that domestic dogs will lick their inguinal region and wounds, but exhibit no elaborate cleaning and grooming.

Licking in the captive coyotes that I observed was directed primarily toward the distal part of the front legs, with occasional licking of shoulders, thighs, and inguinal region being exhibited. Licking the distal part of the hind legs was never observed, although this action probably does occur. Typically, the animals exhibited licking only when lying down.

The frequency of licking appeared to be associated with certain environmental conditions (Table 10). A straw-covered floor, which was dry, promoted very little grooming. The

Table 10. Frequency of self-licking exhibited by coyote D and the condition of the floor.

Condition of Floor	Temperature (^{o}F)	Time Lying While Alert (Minutes)	Time Licking (Minutes: Seconds)	Time Licking Per Hour Lying (Minutes)
Dry, with straw	Below 32^{o}	-	-	-
	Above 32^{o}	351	0:15	0.04
Snow, with straw	Below 32^{o}	109	1:35	0.87
	Above 32^{o}	436	4:20	0.60
Snow, with no straw	Below 32^{o}	217	29:15	8.09
	Above 32^{o}	136	67:25	29.74

presence of snow, however, resulted in a significant increase in self-licking. When the snow was covered with straw, the increase was slight, but elaborate grooming was exhibited when the snow was exposed, especially when the ambient temperature was above freezing.

This type of response appears to be involved when the animal becomes soiled, and is frequently seen in domestic dogs (R. P. Stoneberg, pers. comm.).

Licking as a displacement activity would be exhibited in a high intensity and/or in an irrelevant situation (Hinde, 1966). This, however, was never observed in this study, and probably never is exhibited in captive coyotes. The low frequency of licking exhibited by an alert animal in a dry cage (Table 10) supports this hypothesis. There was also no daily rhythm exhibited.

Rubbing and Rolling

The functional significance of rubbing and rolling in canids appears to have several possible explanations. Kleiman (1966) believes that they should be considered as a means of dispersing scent. Van Wormer (1964) stated that coyotes merely "like" to roll on strong odors. Murie (1940) reported observing five coyotes "cleaning" their fur by vigorously rubbing their throats and muzzles on grass, after feeding on a carcass. This latter observation is the reason I included this behavioral pattern in self-grooming. During this study I did not observe any rubbing or rolling in a definite pattern

of self-grooming.

Behavior Associated With Elimination

Frequency of Elimination

Ozoga and Harger (1966) stated that trailed coyotes, in northern Michigan, averaged one urination every 2.5 miles and one defecation every 6.5 miles. However, neither the temporal frequency of these patterns, nor the sexes of the animals were reported.

In an attempt to assign a frequency rate for elimination in "nature", I utilized the data on general activity of coyote A in captivity. This female averaged approximately 372 stereotyped circuits per hour of activity (Fig. 3). Since the length of each circuit was approximately 30 feet (Fig. 2), the animal travelled 2.2 miles during each hour of activity. By extrapolating these data with the data presented by Ozoga and Harger (1966), the temporal frequency of elimination in "nature" appears as an average of one urination every 70.9 minutes, and one defecation every 184.3 minutes. While these rates are highly artificial, I believe that they are sufficiently accurate for a comparison with the relative rates of elimination which were exhibited by the captive coyotes, assuming the physiological processes remain constant.

The frequency of elimination exhibited by coyotes D, E and F (Table 11) was examined by averaging the data for the two males (coyotes D and F), and then averaging the resultant figure with the data for the female (coyote E). This

Table 11. Frequency of elimination exhibited by coyotes D, E and F.

Animal	Sex	Total Time Active (Minutes)	Number of Urinations	Number of Defecations	Minutes Per Urination	Minutes Per Defecation
D	Male	1290	9	1	143.3	1290.0
F	Male	1493	14	6	106.6	248.8
Total	Male	2783	23	7	121.0	397.6
E	Female	1667	3	3	555.7	555.7
Ave.	50:50				338.4	476.7

procedure treats this litter as a population of coyotes with a 50:50 sex ratio.

The frequency of urination exhibited by coyotes D, E and F showed an average time of 338.4 minutes between each urination pattern, a rate which is 4.77 times smaller than the frequency of micturition in "nature". This reduced frequency of urination in captivity could be a result of the environment, since novel odour-bearing and visual objects are rare in a cage. Kleiman (1966) considers novelty to be a stimulus for urination in male coyotes throughout the year, and in female coyotes during the reproductive season.

Defecation in captivity, however, should not be associated with novelty, since Kleiman (1966) states that coyotes do not use feces as material for marking, although domestic dogs and foxes might. This suggests, all factors being equal, that defecation in captivity should occur at a rate which is similar to defecation in "nature".

When the frequency of defecation exhibited by coyotes D, E and F (Table 11) was analysed, the average time between each pattern was 476.7 minutes, or 2.59 times less frequent than defecation in "nature". This suggests that defecation could be directed toward novel objects, and hence, defecation could be involved in depositing odor.

Behavior Preceding Elimination

Martins and Valle (1964) report that a male domestic dog will always "sniff the target" before assuming the adult

posture of micturition, while the female may omit any olfactory exploration. Information on pre-defecation behavior was unavailable.

Behavior exhibited by coyotes D, E and F prior to elimination (Table 12) showed no statistically significant difference in the presence or absence of olfactory exploration. This suggests that sniffing the ground before elimination occurred 75.8 percent of the time, regardless of the type of elimination. Olfactory exploration, or the lack of it, occurred in both sexes for both elimination types.

The occasional lack of pre-urination exploration in the adult males could be associated with micturition patterns that occurred as autonomic responses in conflict situations (Hinde, 1966). However, it probably indicates that urination in the conditions of captivity was not consistently involved in scent marking.

The occurrence of pre-defecation exploration supports the possibility of feces being involved in the deposition of odor (see "Frequency of Elimination"). Since this exploration was exhibited by both sexes, it is possible that the female could be involved in scent marking, contrary to the opinion of Kleiman (1966).

Postures of Elimination

The postures of elimination exhibited by the captive coyotes (Figs. 22, 23 and 24) were similar to those of the domestic dog (Martins and Valle, 1964; Scott and Fuller, 1965), with the exception of the micturition posture of the

Table 12. Pre-elimination behavior exhibited by coyotes D, E and F.

Pre-Elimination Pattern	Type of Elimination	Number Per Coyote D	E	F	Total
Walk	Urinate	2	1	1	4
Explore	Urinate	7	1	12	20
Walk	Defecate	0	1	3	4
Explore	Defecate	1	2	2	5

Fig. 22. Micturition posture exhibited by juvenile and adult male coyotes in captivity.

Fig. 23. Micturition posture exhibited by juvenile and adult female coyotes in captivity.

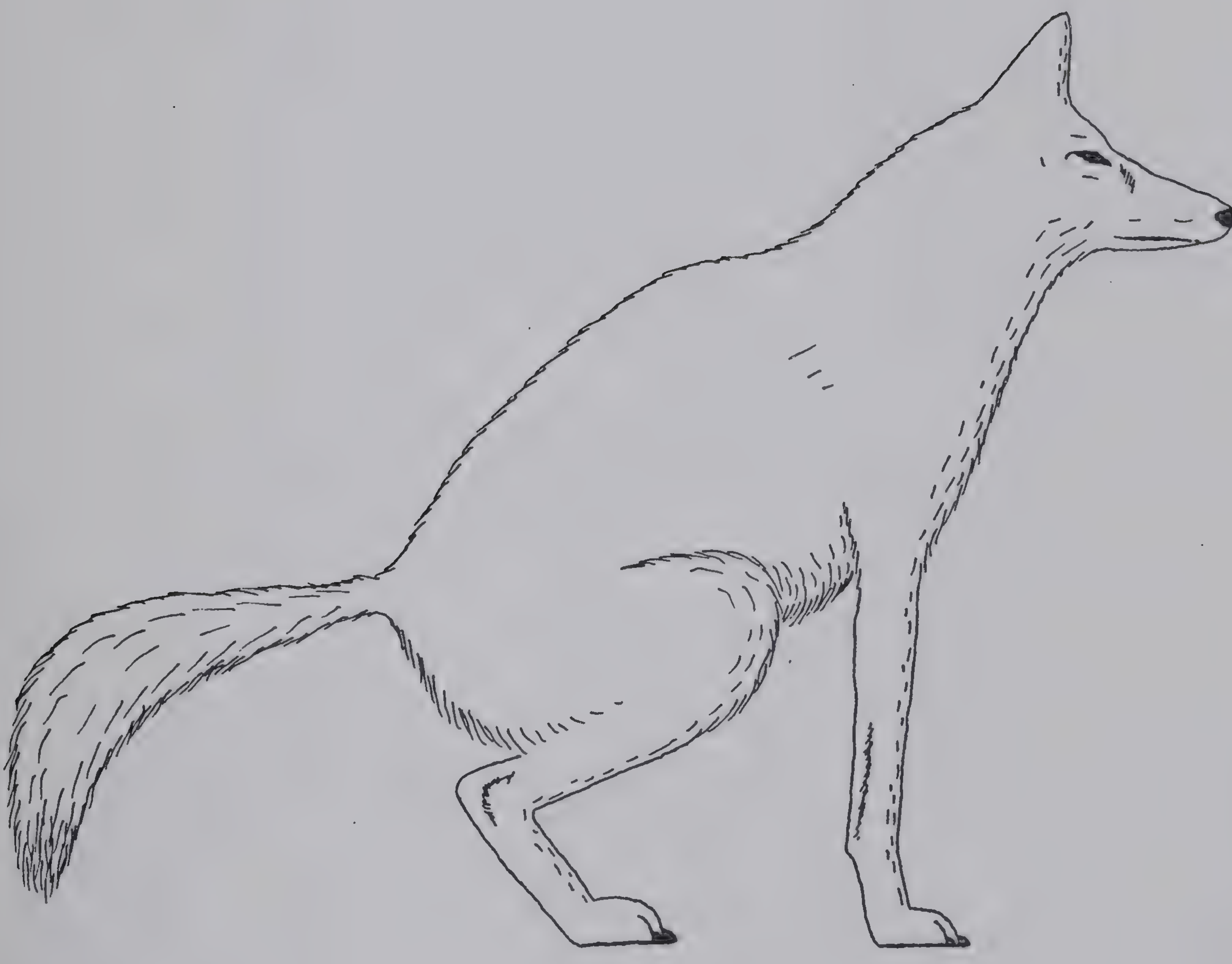
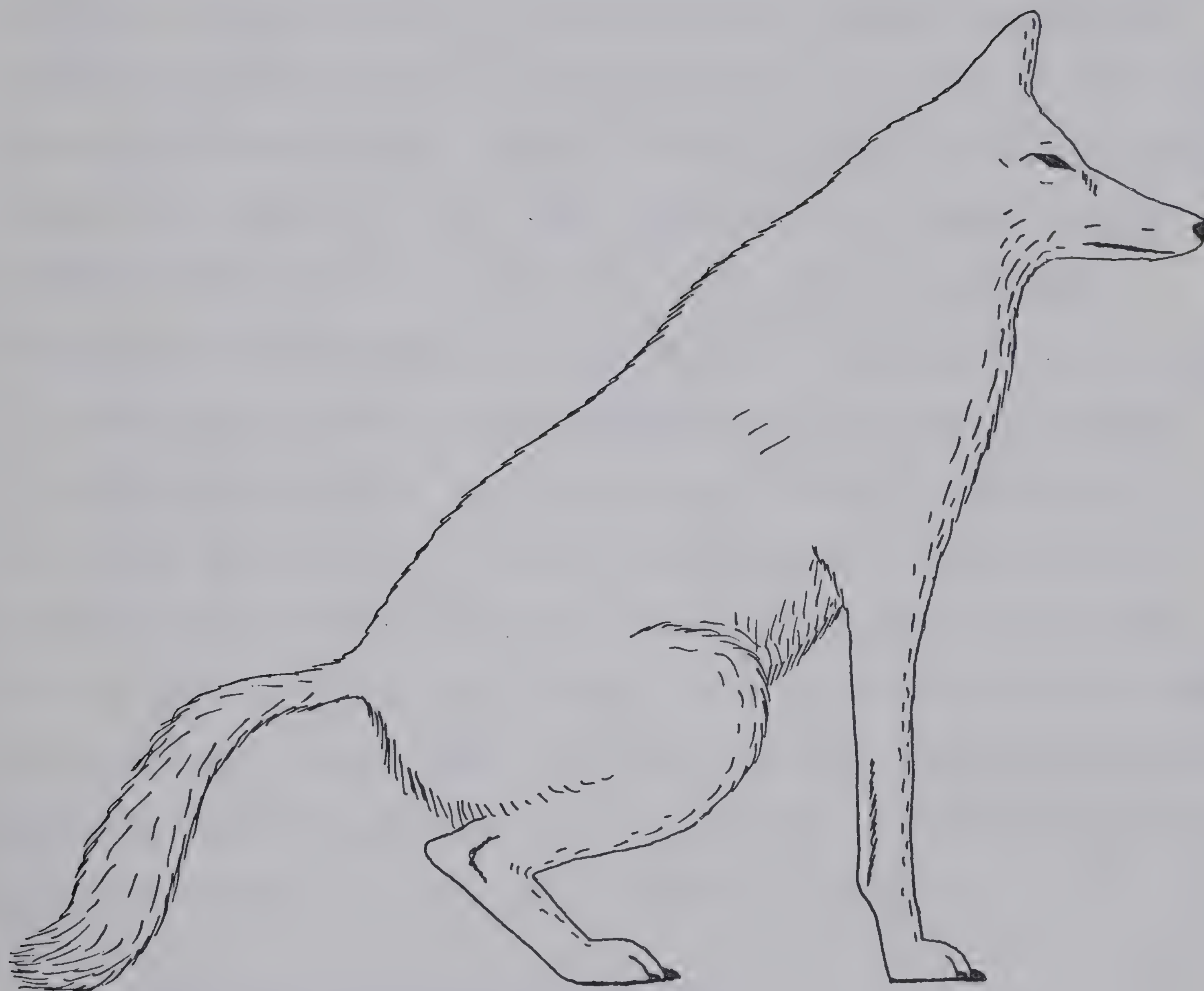


Fig. 24. Defecation posture of coyotes in captivity.



adult male. The adult males observed during this study never displayed the typical leg-lifting that is so familiar with domestic dogs, even though this pattern has been observed in captive coyotes (Dleiman, 1966). Berg (1944) states that leg-lifting is innate and controlled by the amount of testosterone in the body, so the retention of the infantile pattern of urination in the males was probably associated with the conditions of captivity, since yearling coyotes are sexually mature (Snow, 1967). Scott and Fuller (1965) state that male domestic dogs, when confined to an area, rarely exhibit leg-raising. They also state that the primary stimulus of leg-raising is the odor of a strange dog's urine in combination with visual landmarks. This suggests that leg-lifting probably is a ritualized behavior associated with the deposition of scent. However, the occurrence of exploration before urination (Table 12) suggests that the males did use urine as a marker. This suggests that the odor of a strange coyote may provide a stronger stimulus for scent marking than is provided by litter mates, and that leg-lifting occurs only in response to a strong stimulus.

Behavior Following Elimination

The only behavioral pattern exhibited by the captive coyotes following elimination was the presence or absence of olfactory exploration of the elimination site. The lack of any pattern of scratching the ground was probably associated with the conditions of captivity, since Fentress (1967)

noted that a tame wolf exhibited scratching after defecation only when on a strange territory. Typically, though, most males and some females exhibit scratching after urination (Kleiman, 1966), and after defecation (Scott and Fuller, 1965). This suggests that scratching the ground, like leg-lifting (p. 69), could be a ritualized behavior associated with scent marking, although a novel odor is required to elicit both leg-lifting and scratching.

Behavior exhibited by captive coyotes following elimination (Table 13) showed no statistical difference in the presence or absence of olfactory exploration. This suggests that sniffing the ground following elimination occurred 72.7 percent of the time, regardless of the type of elimination.

Elimination Sites

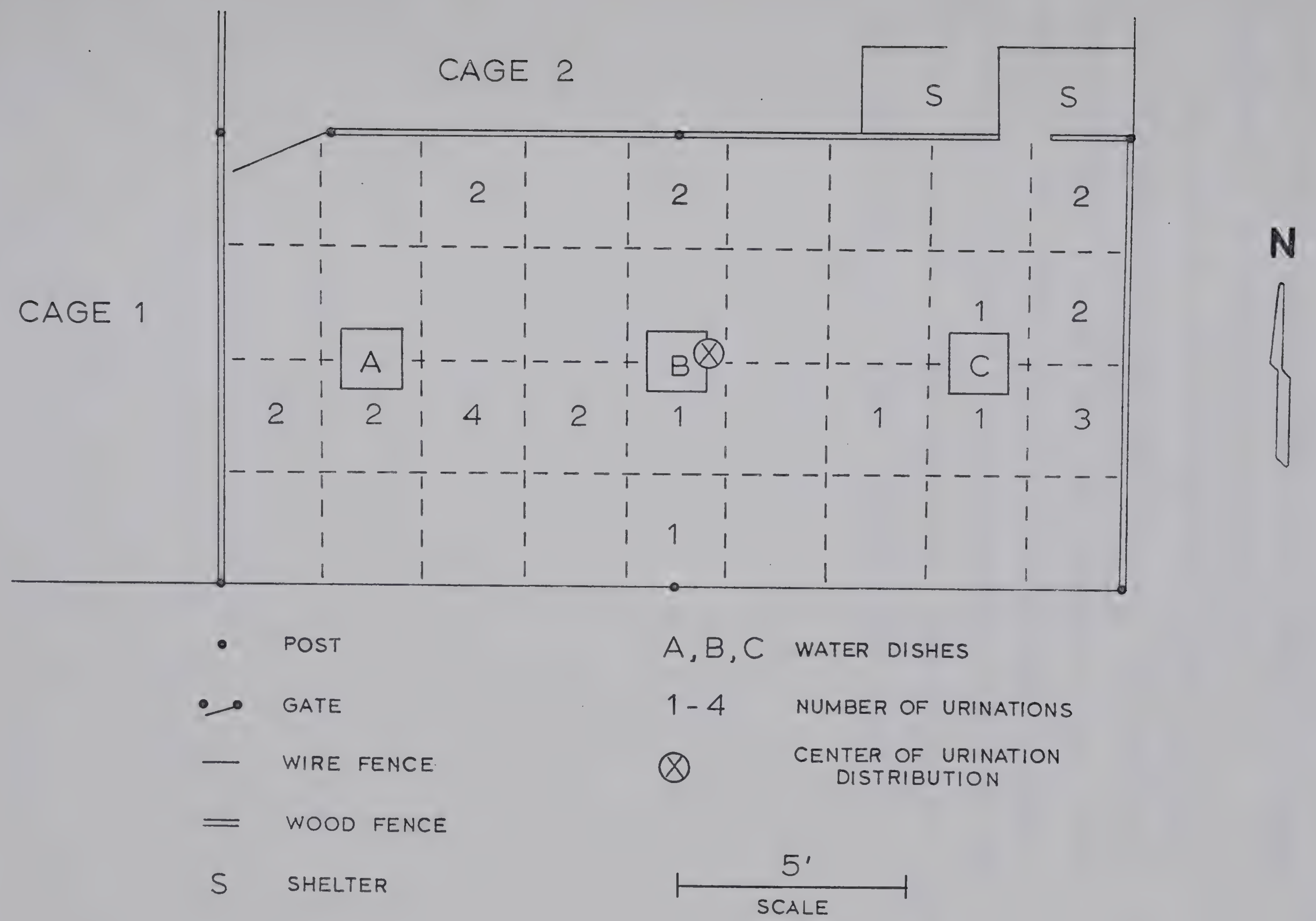
Hediger (1964) states that the elimination sites of many captive predators are "localized", for these sites have a significance as a marking place. During this study, I recorded the observed sites of urination and defecation, and collected the scats for 21 days from cage 3, hoping to establish the location of the "scent posts". This analysis was based on the assumption that cage 3 was large enough for localization of elimination sites to be displayed, if this trait exists.

The urination sites of coyotes D, E and F in cage 3 (Fig. 25) do not appear to exhibit any localization. The

Table 13. Post-elimination behavior exhibited by coyotes D, E and F.

Type of Elimination	Post-Elimination Pattern	Number Per Coyote D	E	F	Total
Urinate	Walk	5	0	1	6
Urinate	Explore	4	2	12	18
Defecate	Walk	1	2	0	3
Defecate	Explore	0	1	5	6

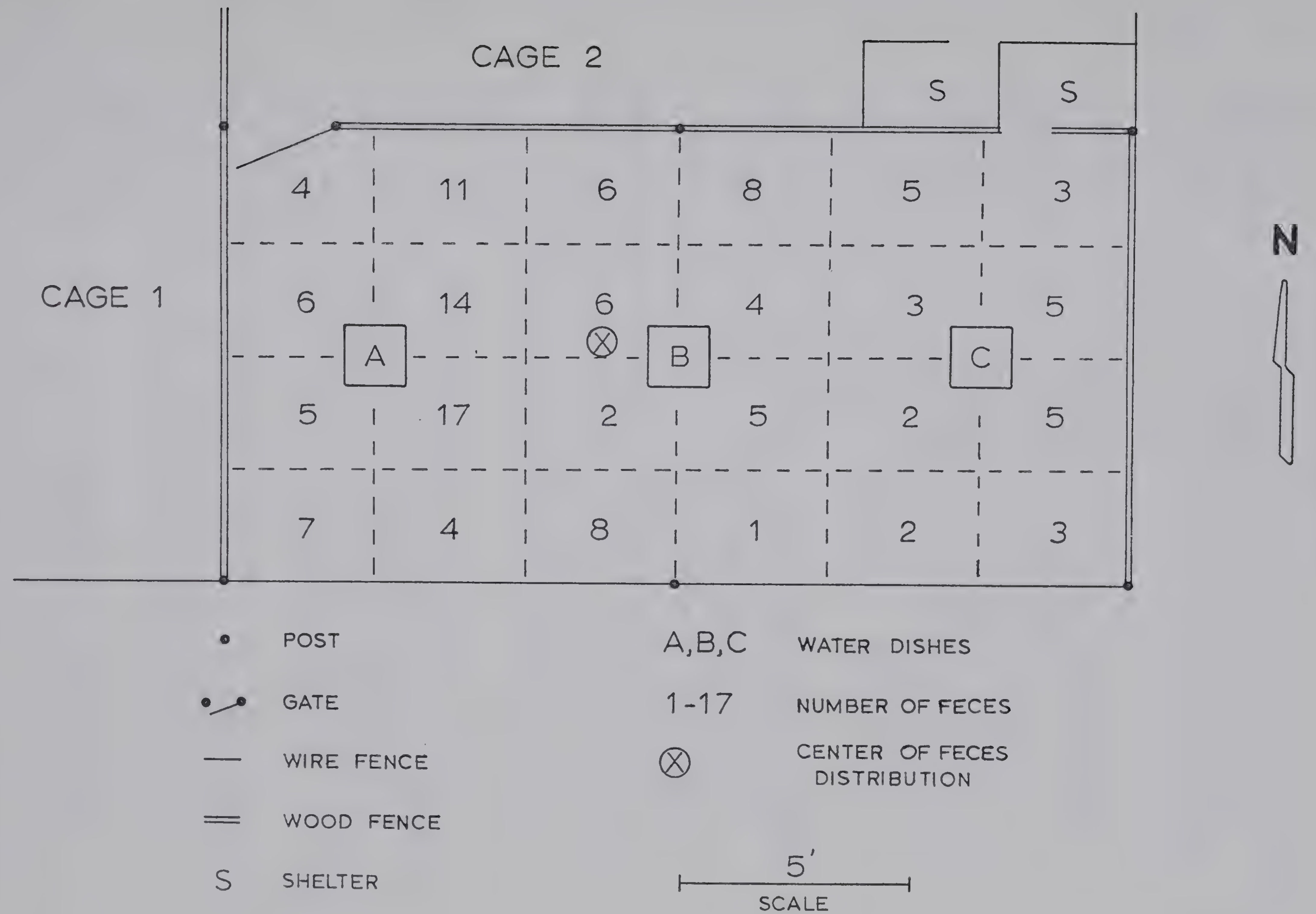
Fig. 25. Micturition sites of coyotes D, E and F in cage 3.


CAGE 1
CAGE 2
S
S
N
A
B
C
2
2
2
2
2
2
4
2
1
1
1
3
1
1
1
POST
GATE
WIRE FENCE
WOOD FENCE
S SHELTER
A, B, C WATER DISHES
1 - 4 NUMBER OF URINATIONS
CENTER OF URINATION DISTRIBUTION
5′
SCALE

center of micturition distribution near the center of the cage and the distribution of urination sites suggests a random occurrence of urination sites in captivity.

The defecation sites of coyotes D, E and F in cage 3 (Fig. 26) appear to exhibit localization. The center of feces distribution suggests a shift towards the west end of the cage. This shift could be associated with the heavy utilization of the east end of the cage as a bed site (Fig. 15), for Young and Jackson (1951) state that coyotes are clean about their dens, with little refuse or odor present.

Fig. 26. Defecation sites of coyotes D, E and F in cage 3 over the period May 14, 1968 to June 3, 1968.


CAGE 2
CAGE 1
S
S
4
11
6
8
5
3
6
14
6
4
3
5
A
B
C
5
17
2
5
2
5
7
4
8
1
2
3
N
POST
GATE
WIRE FENCE
WOOD FENCE
S SHELTER
A,B,C WATER DISHES
1-17 NUMBER OF FECES
CENTER OF FECES DISTRIBUTION
5'
SCALE

CONCLUDING DISCUSSION

Maintenance, or non-social behavior exhibited by coyotes in captivity which I noted during this study consists of the following:

1. The bed site was generally situated in an elevated and/or concealed location in the cage.
2. When lying down, the animals located themselves next to a wall with their backs facing the wall 86 percent of the time. This was probably associated with an element of "security".
3. Coyotes E and F appeared to favor one side of their body when lying down. This trait was examined by suggesting asymmetry in the lengths of the humeri.
4. Meteorological elements appear to be of secondary importance in the location of the bed site, with the structural characteristics of the cage being most important.
5. Turning around before lying down appears to orient the body of the animal for the posture exhibited when lying down, although it occasionally functions in preparing the bed.
6. Pawing the ground before lying down appears to be involved in preparing the bed by making the ground smoother.
7. The posture utilized when lying down appears to be associated with ambient temperature.
8. Huddling behavior of adult coyotes has no relationship

to ambient temperature.

9. Captive coyotes appear to lie down for shorter periods when it is cold than when it is warm.
10. The type of stretch exhibited after a period of inactivity may have social implications.
11. Captive coyotes appear to exhibit a greater number of stretches after an increased period of lying down.
12. Stretching may be associated with heat production through increased muscle tone.
13. Scratching and biting are probably equal in effectiveness for relieving an irritation, and the response exhibited depends on the location of the irritant. The causal factor which elicits scratching or biting appears to be concentrated toward the head of the animal.
14. Self-licking is exhibited when the animal becomes soiled.
15. The frequency of urination and defecation appears to be less in captivity than in "nature". This is probably associated with lack of novelty in a cage.
16. Pre-urination and pre-defecation exploration suggest that both eliminative patterns are involved in scent marking. Both sexes exhibited these patterns.
17. Postures of elimination are similar to those of domestic dogs, although the males never displayed the leg-lifting posture of urination. This was probably associated with lack of novelty in the cage.
18. Scratching the ground was never exhibited after elimination. This was probably associated with lack

of novelty in the cage.

19. Urination sites of coyotes in captivity appear to be randomly distributed in the cage.
20. Defecation sites of coyotes in captivity appear to be located away from the bed site.

The general activity of coyotes in captivity appears to be associated with several meteorological elements, although photoperiod probably influences gross activity to the greatest degree. The circadian rhythm exhibited by coyotes in captivity suggests that these animals are diurnal in their activity, with the peak of activity occurring shortly after dawn. This shift away from the nocturnal pattern of coyotes in nature was probably associated with the availability of food.

Ambient temperature, relative humidity and barometric pressure were each associated with general activity of coyotes in captivity. The coyotes appeared to exhibit the highest levels of activity at 30 to 60°F, low relative humidity and low barometric pressure. The barometric pressure exhibited the closest association with activity.

The relationship between the wind and general activity was examined by restricting the analysis to the association between wind and pressure change, with the resultant influence on activity. It was noted that winds up to 14 miles per hour stimulate activity while higher wind velocities reduce activity, although a major wind with a positive pressure

change resulted in a smaller reduction in activity than a major wind with a negative pressure change.

The only seasonal change in activity occurred during the spring, when there was a significant increase in activity. The causal factor for this increase could be associated with the denning behavior of female coyotes.

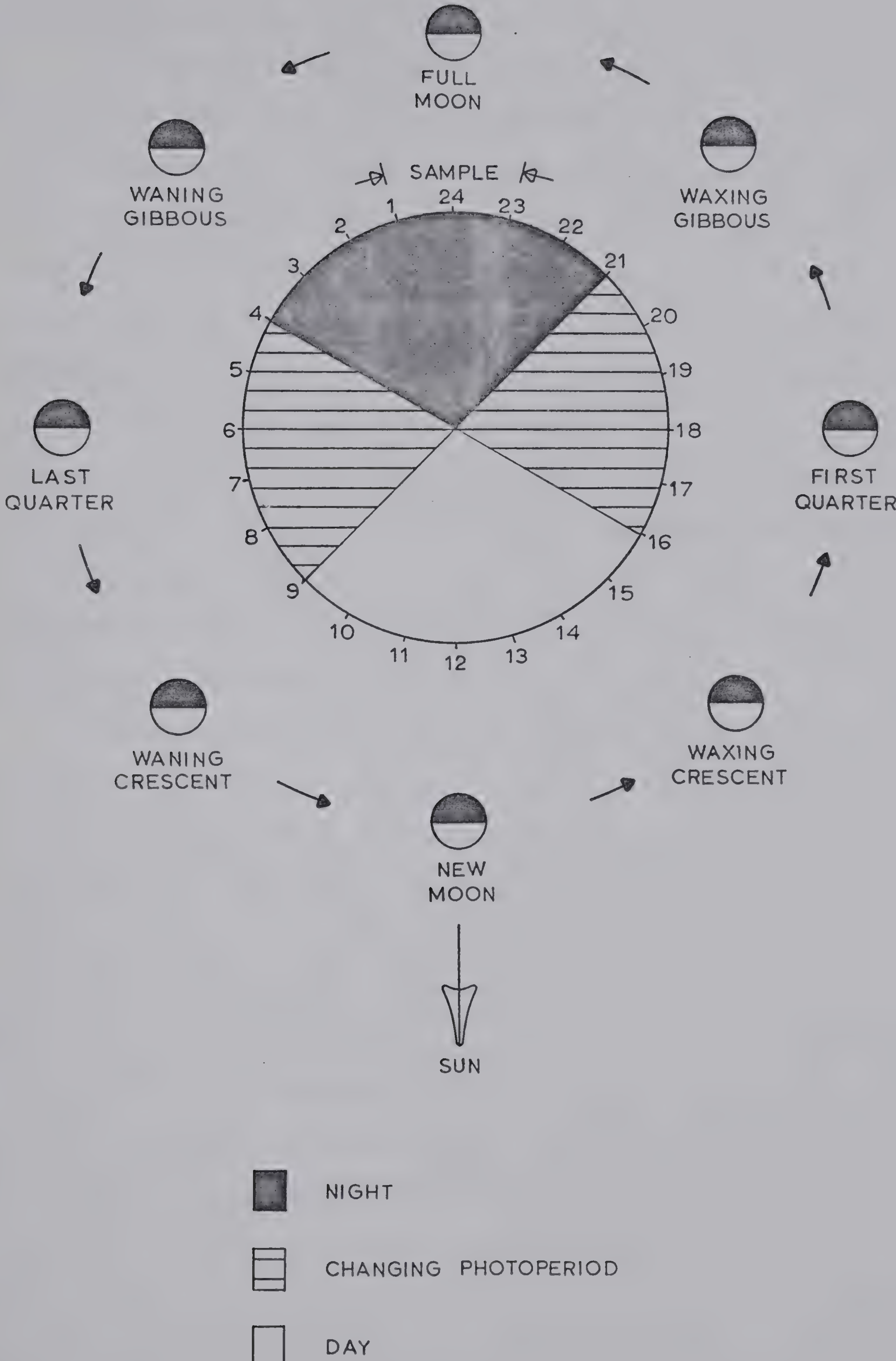
Probably the most prominent association examined during this study was the apparent oscillation in general activity during the lunar cycle, with a significant increase in activity during the full moon. The oscillatory nature of the curve appears to eliminate the possibility that the animals were responding to lunar illumination, since the intensity of light should increase at a linear rate between the new and full moon. A more probable explanation for the nature of the curve would be that the activity patterns of the captive coyotes are associated with some meteorological element which oscillates in a similar fashion during the lunar cycle. However, Namias (1951, p. 819) states that "no one has ever proved in a single case to date, that during or after a given arrangement of the moon or the planets any weather phenomenon occurred more frequently or less frequently than would have been expected from chance." He goes on to remark that "the influence of the moon upon the atmosphere is restricted to producing atmospheric tides, which represent diurnal pressure variations that amount to only 1/1000 of the changes associated with weather developments." Chapman (1951) reports that a multitude of meteorologists have vainly sought for lunar

monthly meteorological variations, and he considers a semi-diurnal oscillation to be more feasible.

In spite of these strong arguments against any lunar influence on the atmosphere, I will attempt to explain the apparent oscillation in activity during the lunar cycle by considering the possibility of a lunar influence on barometric pressure. There are two reasons for this choice. First, the activity of coyote A exhibited a stronger association with barometric pressure than with temperature or relative humidity. The second reason is that of logic. Since the gravitational attraction of the moon is a tide-producing force on the oceans of the world (Rogers, 1960), there is no apparent reason why the moon should not produce tides in the atmosphere, for air, like water, is matter, and matter is subject to variations in the effective gravity.

The procedure followed in analysing the possibility of a lunar influence on the barometric pressure was to restrict the sample period to the times between 2300 and 0100 hours. This two hour period, in essence, holds the sun constant, and at the opposite side of the earth from the study area (Davis and Foote, 1953). The result of this procedure is that the moon is the only tide-producing force that varies at the study site (Fig. 27). This appears to be essential in determining any lunar influence on the atmosphere, for even though the lunar tidal action is 2.4 times as great as the solar tidal action (Chapman, 1951), the combined sun-moon effect would probably have a dampening influence on any

Fig. 27. Temporo-spatial arrangement of the lunar synodic month (adapted from Whipple, 1941, fig. 63) and its relationship with the sample period at Edmonton, Alberta.



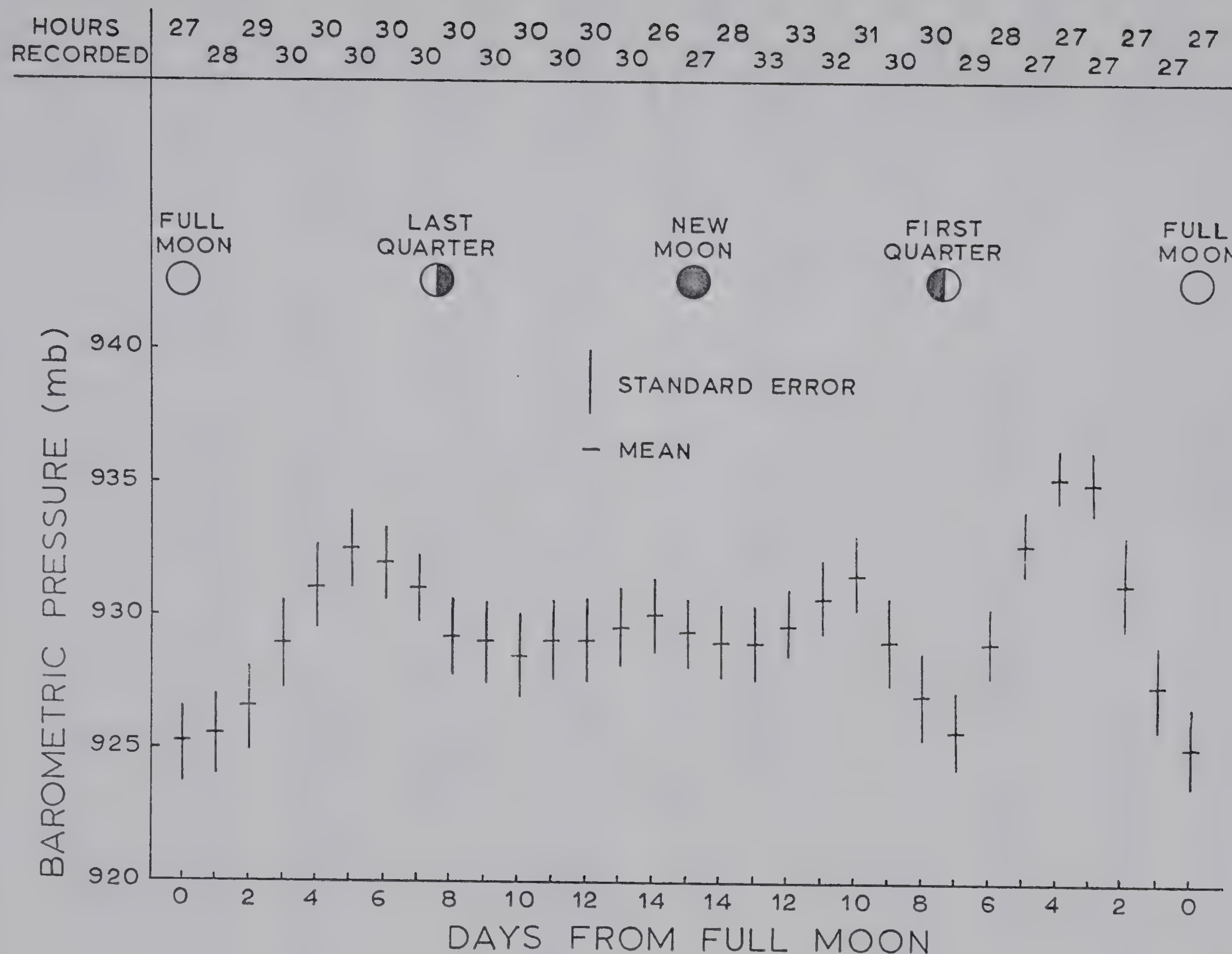
FULL MOON
WAXING GIBBOUS
FIRST QUARTER
WAXING CRESCENT
NEW MOON
WANING CRESCENT
LAST QUARTER
WANING GIBBOUS
SAMPLE
1
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
SUN
NIGHT
CHANGING PHOTOPERIOD
DAY

oscillation that could occur.

Another advantage to utilizing a two hour sample period is that it limits the number of apparent lunar-days that the area is exposed to. Since the rotating earth moves a specific area, in relation to the moon, through every stage of the lunar cycle in a 24 hour day, a 2 hour period would restrict the area to the influence of approximately 2.46 lunar days (Whipple, 1941). The result of this procedure is that during the two hour sample period at any stage of the lunar cycle, the moon will be located at a specific region in relation to the study area. Thus, both the moon and the sun are essentially constant in location for each specific day of the lunar cycle, with each day of the lunar cycle having a different relationship with the location of the moon (Fig. 27).

The resultant data (Fig. 28) suggest an oscillation of barometric pressure as the moon travels around the earth. This oscillation, when correlated with the oscillation exhibited by the activity of coyote A (Fig. 14), gives a significant correlation of -0.4832. This relationship is a similar to the negative correlation obtained when activity was related to the barometric pressure (see "Activity and the Barometric Pressure"). This suggests that the moon may produce an oscillation in barometric pressure which may in turn have been associated with some changes in activity recorded during this study.

Fig. 28. Lunar cycle and barometric pressure recorded from 2300 to 0100 hours (mean values, and pooling the values from each lunar day with the adjacent days) over the period July 22, 1967 to June 2, 1968.



HOURS RECORDED
27 28 29 30 30 30 30 30 30 30 30 30 30 30 26 27 28 33 33 32 31 30 30 29 28 27 27 27 27 27
FULL MOON
LAST QUARTER
NEW MOON
FIRST QUARTER
FULL MOON
STANDARD ERROR
MEAN
BAROMETRIC PRESSURE (mb)
940
935
930
925
920
0 2 4 6 8 10 12 14 14 12 10 8 6 4 2 0
DAYS FROM FULL MOON

LITERATURE CITED

Ables, E.D. 1969.
Activity studies of red foxes in southern Wisconsin. J. Wildl. Mgmt., 33:145-153.

Allen, D.L. and L.D. Mech. 1963.
Wolves versus moose on Isle Royale. National Geographic Magazine, 123:200-219.

Berg, I.A. 1944.
Development of behavior: the micturition pattern in the dog. J. Exp. Psychol., 34:343-368.

Berlyne, D.E. 1960.
Conflict, arousal and curiosity. McGraw-Hill Book Co., Inc., New York.

Bider, J.R. 1962.
Dynamics and the temporo-spatial relations of a vertebrate community. Ecology, 43:634-646.

Brody, S. 1945.
Bioenergetics and growth. Reinhold Pub. Corp., New York.

Brown, F.A., Jr., M.F. Bennett, H.M. Webb and C.L. Ralph. 1956.
Persistent daily, monthly and 27-day cycles of activity in the oyster and quahog. J. Exp. Zool., 131:235-262.

Brown, F.A., Jr., H.M. Webb and E.J. Macey. 1957.
Lag-lead correlations of barometric pressure and biological activity. Bio. Bull., 113:112-119.

Chapman, S. 1951.
Atmospheric tides and oscillations. In T.F. Malone (ed.), Compendium of meteorology. Waverly Press, Inc., Baltimore. 510-530.

Cowgill, U.M., A. Bishop, R.J. Andrew and G.E. Hutchinson. 1962.
An apparent lunar periodicity in the sexual cycle of certain prosimians. Proc. Nat. Acad. Sci., 48:238-241.

Davis, R.E. and F.S. Foote. 1953.
Surveying, theory and practice. McGraw-Hill Book Co., Inc., New York.

Dewan, E. 1968.
Improvement in reliability of rhythm method discovered. News item in the Edmonton Journal, December 19, 1968.

Dobie, J.F. 1961.
The voice of the coyote. A Bison Book, Univ. of Nebraska Press.

Fentress, J.C. 1967.
Observations on the behavioral development of a hand-reared male timber wolf. Am. Zoologist, 7:339-351.

Gerstell, R. 1942.
The place of winter feeding in wildlife management. Res. Bull. No. 3, Penn. Game Comm., Harrisburg. 1-121.

Gier, H.T. 1957.
Coyotes in Kansas. Kansas Agr. Expt. Sta. Bull. 393.

Hamilton, W.J., Jr. 1939.
American mammals. McGraw-Hill Book Co., Inc., New York.

Hediger, H. 1964.
Wild animals in captivity. Dover Publ., Inc., New York.

Hinde, R.A. 1966.
Animal behavior, a synthesis of ethology and comparative psychology. McGraw-Hill Book Co., Inc., New York.

Hoar, W.S. 1966.
General and comparative physiology. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Jolicoeur, P. 1963.
Bilateral symmetry and asymmetry in limb bones of <u>Martes americana</u> and man. Rev. Can. Biol., 22:409-432.

Jolly, A. 1966.
Lemur behavior, a Madagascar field study. U. of Chicago Press, Chicago.

Kleiman, D. 1966.
Scent marking in the Canidae. <u>In</u> P.A. Jewell and C. Loizos (eds.), Play, exploration and territory in mammals. Symp. of Zool. Soc. of London No. 18. 167-177.

Levine, N.D., M.N. Krehna, D.T. Clark, and I. Aves. 1960.
Comparison of nematode egg counting techniques for cattle and sheep feces. Amer. J. Vet. Res., 21:511-515.

Marler, P. and W.J. Hamilton, III. 1967.
Mechanisms of animal behavior. John Wiley and Sons, Inc., New York.

Martins, T. and J.R. Valle. 1964.
Hormonal regulation of the micturition behavior of the dog. <u>In</u> S.C. Ratner and M.R. Denny (eds.), Comparative psychology, research in animal behavior. Dorsey Press, Illinois. 339-350.

Murie, A. 1940.
Ecology of the coyote in the Yellowstone. U.S. Dept. of Int., Natl. Park Serv., Fauna Ser. 4.

Murie, A. 1944.
The wolves of Mount McKinley. U.S. Dept. of Int., Natl. Park Serv., Fauna Ser. 5.

Namias, J. 1951.
General aspects of extended-range forecasting. In T.F. Malone (ed.), Compendium of meteorology. Waverly Press, Inc., Baltimore. 816-824.

Orr, H.D. 1959.
Activity of white-footed mice in relation to environment. J. Mammal., 40:213-221.

Ozoga, J.J. and E.M. Harger. 1966.
Winter activities and feeding habits of northern Michigan coyotes. J. Wildl. Mgmt., 30:809-818.

Petterssen, S. 1958.
Introduction to meteorology. McGraw-Hill Book Co., Inc., New York.

Rogers, E.M. 1960.
Physics for the inquiring mind; the methods, nature, and philosophy of physical science. Princeton Univ. Press, New Jersey.

Rutter, R.J. and D.H. Pimlott. 1968.
The world of the wolf. J.B. Lippincott Co., New York.

Scott, J.P. 1967.
The evolution of social behavior in dogs and wolves. Am. Zoologist, 7:373-381.

Scott, J.P. and J.L. Fuller. 1965.
Genetics and the social behavior of the dog. Univ. of Chicago Press.

Sealander, J.A., Jr. 1952
The relationship of nest protection and huddling to survival of Peromyscus at low temperatures. Ecology, 33:63-71.

Siivonen, L. and J. Koskimies. 1955.
Population fluctuations and the lunar cycle. Papers on Game Res., Finnish Game Foundation, 14:1-22.

Snow, C.J. 1967.
Some observations on the behavioral and morphological development of coyote pups. Am. Zoologist, 7:353-355.

Soper, J.D. 1964.
The mammals of Alberta. The Hamly Press Ltd., Edmonton, Alberta.

Sperry, C.C. 1941.
Food habits of the coyote. U.S. Dept. Int., Fish and Wildlife Service, Wildl. Res. Bull., 4:1-70.

Sprott, R.L. 1967.
Barometric pressure fluctuations: effects on the activity of laboratory mice. Science, 157:1206-1207.

Steel, R.G.D. and J.H. Torrie. 1960.
Principles and procedures of statistics, with special reference to the biological sciences. McGraw-Hill Book Co., Inc., New York.

Van Wormer, J. 1964.
The world of the coyote. J.B. Lippincott Co., New York.

Walker, B.W. 1952.
A guide to the grunion. Calif. Fish and Game, 38:409-420.

Whiteman, E.E. 1940.
Habits and pelage changes in captive coyotes. J. Mammal., 21:435-438.

Whipple, F.L. 1941.
Earth, moon and planets. The Blakiston Co., Philadelphia.

Young, S.P. and E.A. Goldman. 1944.
The wolves of North America, I-II. Dover Publ., Inc., New York.

Young, S.P. and H.H.T. Jackson. 1951.
The clever coyote. Wildl. Mgmt. Inst., Washington, D.C.

APPENDICES

Appendix 1. Coordination of the periods of general activity or inactivity of coyotes A, D and E during 50 hours of observation over the period May 10, 1969 to May 19, 1969.

Date	Start Observation (Time)	Observation Time (Minutes)	Coordinated Activity or Inactivity (Minutes)
May 10	0640	180	172
10	1240	120	38
11	0715	180	159
11	1240	315	226
12	0545	90	62
12	1140	135	66
13	0530	105	105
13	1110	120	75
14	0535	100	98
14	1150	130	127
15	0535	95	94
15	1130	135	69
16	0540	80	52
16	1100	215	138
17	0715	80	80
17	1455	320	218
18	0725	90	90
18	1425	335	178
19	0655	175	153
Total		3000	2200

Appendix 2. Observation schedule of the behavioral study of coyotes D, E and F over the period December 3, 1967 to May 11, 1968.

Date		Observation Time (Minutes Per Hour) 5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
December	3									45	60	60	10					175
	4				15	60	50											125
	8				5	60	10	45	45									165
	10									20	60	10						90
	29							30	60									90
	31									35	60							95
January	6								60	45								105
	7											30	50					80
	8								45	60	60	60	15					240
	18										45	60						105
	19						60	60	35									155
	23				5	60	60	60	40	60	25							310
	25							15	60	50								125
	26				10	60	60	45										175
February	6						15	60	50									125
	8									15	60	20						95
	9					55	60	45										160
	15							25	60	40	45	5						175
	29								35	60	60	30	60	60				305
March	5						10	60	60									130
	7								35	60	60							125
	11								45	60	25							130
	14									60	60	55						175
	18				15	60	55											130
	26								45	60	25							130

(continued)

Appendix 2. Continued.

Date		Observation Time (Minutes Per Hour) 5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
April	2									30	60	50						140
	4			60	60	35												155
	6					50	60	30					45	60	55			300
	8				55	20												75
	9				15	60	25											100
	12			55	60	35												150
	13							35	60	60	55							210
	15									30	60	30						120
	16					10	60	60	55	35	50							270
	17	10	60	60	15													145
	18										20	60	5					85
	20								55	60	15	60	40					230
	21													5	60	25		90
	23									30	60	60	35	60	60			305
	24				35	60	35						25	60	10			225
	25					30	60	45										135
	29		50	60	35	30	60	45										280
May	2							60	55	55	60							230
	3								30	60	60	30						180
	8									35	60	20						115
	9				45	60	20	60	60									245
	10									55	60	5						120
	11														60	60	35	155
Total		10	110	235	370	745	700	780	990	1120	1175	645	285	245	245	85	35	7775

Appendix 3. Diurnal-nocturnal distribution of general activity of coyote A recorded during varying photoperiods over the period July 22, 1967 to June 2, 1968.

	Day Activity			Night Activity				
Day Length (Hours)	Hours Recorded	Mean Hourly Activity	Mean Day Activity	Hours Recorded	Hourly Activity	Mean Night Activity	Mean Daily Activity	% Day Activity
7	196	125.9	881.3	547	27.0	459.0	1340.3	65.8
8	79	198.5	1588.0	206	56.0	896.0	2484.0	63.9
9	69	179.4	1614.6	236	27.0	405.0	2019.6	80.0
10	227	76.4	764.0	378	16.2	226.8	990.8	77.1
11	330	153.0	1683.0	453	45.8	595.4	2278.4	73.9
12	154	138.4	1660.8	180	33.7	404.4	2065.2	80.4
13	523	103.5	1345.5	540	56.0	616.0	1961.5	68.6
14	68	108.3	1516.2	69	49.0	490.0	2006.2	75.6
15	528	108.0	1620.0	417	61.9	557.1	2177.1	74.4
16	153	48.1	769.6	98	22.7	181.6	951.2	80.9
17	278	135.3	2300.1	123	86.8	607.6	2907.7	79.1
Total	2605	117.2	1431.2	3247	42.5	494.4	1925.6	74.3

Appendix 4. Barometric pressure and ambient temperature recorded from 2200 to 0300 hours (mean values, and pooling the values from each pressure group with the adjacent groups) over the period July 22, 1967 to June 2, 1968.

Barometric Pressure (mb)	Hours Recorded	Ambient Temperature (^{o}F) Mean	Standard Error
910.0 - Less	4	36.8	3.6
910.1 - 912.0	6	42.7	5.3
912.1 - 914.0	13	42.5	3.5
914.1 - 916.0	18	42.2	2.7
916.1 - 918.0	30	36.2	2.1
918.1 - 920.0	32	33.6	1.9
920.1 - 922.0	50	29.0	1.5
922.1 - 924.0	56	31.0	2.5
924.1 - 926.0	67	31.2	2.3
926.1 - 928.0	71	34.4	2.2
928.1 - 936.0	81	35.0	1.9
930.1 - 932.0	82	34.8	1.9
932.1 - 934.0	74	33.0	1.9
934.1 - 936.0	69	29.1	2.2
936.1 - 938.0	57	27.6	2.2
938.1 - 940.0	49	27.5	2.5
940.1 - 942.0	34	23.5	3.2
942.1 - 944.0	27	19.4	3.8
944.1 - More	16	14.0	4.7

Appendix 5. Barometric pressure and relative humidity recorded from 2200 to 0300 hours (mean values, and pooling the values from each pressure group with the adjacent groups) over the period July 22, 1967 to June 2, 1968.

Barometric Pressure (mb)	Hours Recorded	Relative Humidity (%) Mean	Standard Error
914.0 - Less	17	81.5	3.8
914.1 - 916.0	23	81.0	3.0
916.1 - 918.0	30	81.4	2.7
918.1 - 920.0	33	83.2	2.4
920.1 - 922.0	50	83.6	2.0
922.1 - 924.0	56	83.1	1.9
924.1 - 926.0	66	83.5	1.6
926.1 - 928.0	70	86.4	1.5
928.1 - 930.0	80	87.6	1.3
930.1 - 932.0	82	87.4	1.3
932.1 - 934.0	74	84.8	1.6
934.1 - 936.0	69	84.6	1.6
936.1 - 938.0	58	87.0	1.7
938.1 - 940.0	49	87.9	1.6
940.1 - 942.0	34	88.0	1.8
942.1 - 944.0	26	84.4	2.1
944.1 - More	16	86.1	2.0

Appendix 6. General activity of coyote A recorded during each month and season over the period July 22, 1967 to June 2, 1968, with associated pressure and temperature data.

Month and Season	Mean Hourly Activity	Mean Pressure (mb)	Mean Temperature (^{o}F)
July	-	-	-
August	77.3	932.8	51.9
September	68.3	927.9	46.5
October	78.2	926.1	35.3
November	-	-	-
December	66.7	928.2	30.7
January	62.5	929.7	2.4
February	43.8	934.3	12.0
March	92.7	928.9	28.9
April	96.5	927.8	30.7
May	109.3	930.0	41.4
June	-	-	-
Autumn	69.6	-	-
Winter	57.0	-	-
Spring	99.5	-	-
Summer	66.7	-	-

Appendix 7. Location of bed and orientation of body exhibited by coyotes D, E and F when lying down in cage 3 over the period December 8, 1967 to May 11, 1968.

Cage Location	Observed Time Lying Down (Minutes)								Total
	Clockwise				Counterclockwise				
	Back North	Back East	Back South	Back West	Back North	Back East	Back South	Back West	
A - 1	3			239	223			97	562
2		9	3	207	41	1		276	537
3			63	109			3	288	463
4				119				156	275
5	57			123	224			3	407
6			4					9	13
7	6								6
8									0
9	48				69				117
10									0
11									0
12	25	3	39		11		1		79
B - 1	9				65				74
2									0
3		8			60	58		43	169
4									0
5					2				2
6									0
7									0
8									0
9									0

(continued)

Appendix 7. Continued.

Cage Location	Observed Time Lying Down (Minutes) — Clockwise: Back North	Clockwise: Back East	Clockwise: Back South	Clockwise: Back West	Counterclockwise: Back North	Counterclockwise: Back East	Counterclockwise: Back South	Counterclockwise: Back West	Total
B -10									0
11									0
12									0
C - 1	4				1				5
2					25			4	29
3									0
4	23					61			84
5	4	2				168			174
6	7								7
7		4							4
8	147	54	2			48	60	6	317
9	225	1254			584	308			2371
10	23	927	2		8	651			1611
11	66	532	3			766	2		1369
12	186	162	33		3	549	11		944
Total	833	2955	149	797	1316	2610	77	882	9619

Appendix 8. Behavior exhibited by coyotes D, E and F before assuming a posture of inactivity.

Pattern*	Number of Events Per Animal Coyote D	Coyote E	Coyote F	Total
W - S	62	55	64	181
W - L	32	29	16	77
Sn - S	18	36	73	127
Sn - L	161	101	48	310
W - T - S	7	1	3	11
W - T - L	17	3	12	32
Sn - T - S	1	3	16	20
Sn - T - L	44	21	44	109
P	24	5	21	50
S - L	6	27	27	60
S - T - L	17	18	50	85
L - T - L	33	13	50	96
Misc.	22	10	23	55

* W = walk
Sn = olfactory investigation
S = sit down
L = lie down
T = turning around
P = pawing the ground